TRANSACTIONS OF

THE ROYAL SOCIETY OF CANADA

SECTION V
BIOLOGICAL SCIENCES

THIRD SERIES—VOLUME XLVII—SECTION V

JUNE, 1953

OTTAWA
THE ROYAL SOCIETY OF CANADA
1953

TABLE OF CONTENTS

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA
VOLUME XLVII : SERIES III : JUNE, 1953
SECTION FIVE

PRESIDENTIAL ADDRESS

On Some Fundamental Problems in the Biology of Pacific Salmon

W. A. CLEMENS, F.R.S.C.

MANY investigations have been carried out over the past forty years on the five species of Pacific salmon, genus *Oncorhynchus*, occurring on the North American coast. Many of these studies have been fact-finding in character with the objective of providing information for the management of the fisheries based upon the populations of these species. At the same time, basic biological problems have been given considerable attention and a few of these will be discussed briefly in this paper.

Origin, Distribution, and Speciation

The evolution of the salmonoid fishes probably began in the Eocene period and the genera *Salmo* and *Oncorhynchus* were distinct by the Miocene. Apparently the majority of ichthyologists today accept the separation of the genera *Salmo* and *Oncorhynchus*. Regan (1914) believed that the two genera were not separable but Tchernavin (1938) presented evidence supporting their distinctness.

Of the evolution of the species of *Oncorhynchus* one can only speculate. Tchernavin (1939) indicates a freshwater origin for the genus *Salmo*. If this theory is accepted, the genus *Oncorhynchus* is undoubtedly also of freshwater origin and species formation may be visualized through isolation in river systems with subsequent acquisition of sea-going habits and spread to numerous river systems. Retention of distinct spawning times or locations would prevent extensive hybridization.

On the coast of North America five species of *Oncorhynchus* are recognized, namely: *tchawytscha* (spring, king, chinook), *kisutch* (coho, silver), *gorbuscha* (pink, humpback), *keta* (chum, dog), and *nerka* (sockeye, red, blueback). On the coast of Asia several additional species have been described, some of which are probably of subspecific rank. The following remarks are confined to the North American species.

The five species of *Oncornynchus* mentioned above are separable on the basis of many morphological characters such as numbers of scales in rows along the sides of the bodies, numbers of gill rakers, branchiostegals, fin rays, pyloric caeca, coloration, and of differences in behaviours and life histories (Clemens, 1935; Foerster and Pritchard, 1935; Milne, 1948). These specific differences may have been established through isolation of populations of the original *Oncorhynchus* stock in early Pleistocene and subsequent years. That the separation of the species may have been of comparatively recent date is indicated by the fact that cross-breeding is possible, as shown by the cross-fertilization experiments carried out by Foerster (1935). His results show that of twenty possible crosses five were excellent or good, four were moderately good, and eleven were poor or failures. Only between sockeye and chum salmon were the reciprocal crosses good as shown by the following:

Male	*Female*	
sockeye	chum	good
chum	sockeye	good
sockeye	spring	poor
spring	sockeye	excellent
chum	pink	excellent
pink	chum	poor
pink	spring	excellent
spring	pink	moderate

Hourston (1949), in a preliminary study of the serological relationships among some of the species, finds a fairly close similarity among coho, spring, and sockeye and a significant difference between the chum and the above-mentioned three species.

Brett (1952), in a study of temperature tolerance among young Pacific salmon, determined that the upper lethal temperatures were: spring, 25.1°C.; coho, 25.0°C.; sockeye 24.4°C.; pink, 23.9°C.; and chum, 23.8°C.

On the basis of morphological, physiological, life-history, and behaviour studies to date, it appears that spring and coho salmon are related on the one hand, pink and chum on the other, and that sockeye occupy a position more or less intermediate between the two pairs.

A promising line of investigation on the origin and relations of the species is indicated by the study of chromosome numbers in Salmonidae by Svärdson (1945). He finds that the diploid chromosome number of the Atlantic salmon, *Salmo salar*, is 60 and of the brown

trout, *S. trutta*, 80. He postulates that the basic number in the Salmonidae must have been 10 and the present day salmonoids must accordingly be high-polyploids. His conclusions are as follows:

Salmo salar, Atlantic salmon	6 ×	= 60
S. trutta, brown trout	8 ×	= 80
S. alpinus, Arctic char	8 ×	= 80
S. fontinalis, speckled char	8 × + 4	= 84
Coregonus lavaretus, whitefish	8 ×	= 80
C. albula, whitefish	8 ×	= 80
Thymallus thymallus, grayling	10 × + 2	= 102

Makino (1937) stated that the diploid chromosome number for the chum salmon, *O. keta*, was 74. Svärdson believes this to be of the correct order of magnitude but not quite exact. Mr. James G. Robertson, a graduate student in the Department of Zoology, University of British Columbia, obtained a count of 38 chromosomes for this species but again this is probably not accurate and it is uncertain whether this is a haploid or a diploid number.

It is not improbable that the Pacific salmon are polyploids. If so, at least some of the species may have originated by polyploidy rather than by micromutations. On this basis it may be predicted that the pink salmon will be found to have the smallest chromosome number as it is the smallest of the five species, averaging but four pounds in weight. On the other hand, the spring salmon will be expected to have the largest chromosome number as it is the largest in size and may reach a weight of over 100 pounds.

On the basis of the conception of polyploidy in *Oncorhynchus*, the results of Foerster's cross-fertilization experiments and Hourston's serological studies are not necessarily in conflict in regard to the relationship between sockeye and chum salmon. The crosses between these two species were very successful and this may have been the result of compatibility in chromosome numbers while the difference in the nature of the serum proteins may not have been critical.

It may be conceived that a number of species of *Oncorhynchus* evolved early in the Pleistocene and became distributed along the west coast of North America from Alaska to California. What may have been the distribution of the various species during most of this period is difficult to visualize. The only fossil record of *Oncorhynchus* of which I am aware is that given by Hay (1929) for Pleistocene beds in Oregon. However, from the time of the last glacial period onward, a reasonably clear picture of events may be developed. At the height of the last glacial period, some 15,000 years ago, there could have been no streams from the southern area of Alaska to the northern

section of the State of Washington. The Yukon Valley was not glaciated and it is possible that some species of Pacific salmon were able to spawn in, and the young to survive in, the Yukon River. To the south, the Columbia and other rivers at least as far south as the Sacramento were available and undoubtedly were utilized. If northern and southern populations existed, they probably remained isolated as distinct stocks for many thousands of years. As the glacial ice retreated, innumerable streams came into existence in the region between the Yukon and Columbia rivers and gradually became occupied by the various species. Today the spring salmon has a distributional range from the Sacramento to the Yukon River.

There can be no doubt of the survival of the salmon in the streams to the south and of their dispersal northward, based on knowledge of existing ocean currents and of salmon movements. Survival in the Yukon is uncertain although seemingly possible. Whether dispersal took place southward is also uncertain. Knowledge of ocean currents in the northern area is relatively meagre as is knowledge of the movements of the far northern salmon.

If intermingling of the far northern and the far southern stocks did not occur, distinct racial characters may have developed. A critical study of populations from the southern to the northern limits of distribution might well reveal considerable differences, even in subspecific rank.

Because of the strong homing tendency among some of the species, gene flow throughout their ranges is undoubtedly limited. For the sockeye salmon which exhibit the homing tendency so strongly, there may well be a tendency for racial differences to be superceded by subspecific differences among the populations of some of the widely differing river systems. This may be true even within major river systems because of their almost invariable return to specific streams. At the same time it may be expected that closely similar streams will tend to have closely similar sockeye since the environments will steadily select any genetic variations in the same direction. The unravelling of this taxonomic complex of species with their possible subspecies, races, and ecads is an imposing task. While the problem is of scientific interest, it has an important relation to attempts to establish or re-establish populations. If over a period of some 15,000 years the various populations in the Fraser River system have become adjusted to specific environmental conditions, it may be impossible to transfer successfully eggs or fry between quite diverse environments. For example, the Cultus Lake sockeye are of small size, the average egg production per female is 4,130, the fish travel only 100 miles from

the sea to the spawning ground at an elevation of 190 feet above sea level and spawn for the most part on the gravel beaches at the head of the lake. On the other hand the Chilko Lake sockeye, which are approximately the same size, have an average egg production per female of only 2,700, the fish travel 400 miles to the spawning ground at an elevation of 3,900 feet and spawn in the Chilcotin River below the lake. The young, upon emergence from the gravel, are carried downstream to an area of slow water and some weeks later ascend the river and enter Chilko Lake (Broadhead, 1949). Such differences may have a genetic basis, but they may be only manifestations of a plastic or variable organization which has rather wide ranges of physiological activity and behaviour. It would be well to know the nature of the material being dealt with in fish management procedures.

Migration

The migrations of Pacific salmon have received attention over a long period of years. From 1919 onward a large body of knowledge of the movements of salmon in the ocean and to their spawning areas has been accumulated by means of tagging of sea-living fish and of clipping the fins of seaward migrants. However, it is only in very recent years that the fundamental factors involved in the phenomena of seaward and return migrations have become evident. While the investigations of Dr. A. G. Huntsman in Canada and of Dr. M. Fontaine and associates in France have contributed much to an understanding of the migrations of both anadromous and catadromous fishes, it is the studies of Dr. W. S. Hoar of the University of British Columbia that have provided information specific to the seaward migrations of Pacific salmon. The following account of the behaviour of the juveniles is based upon the publications of Hoar (1951, 1952, 1953).

Sockeye salmon spawn usually in streams tributary to lakes. The fry upon emerging from the gravel are negatively phototactic and remain during the day at the bottom of the streams, where the light is of low intensity. They rise in the water when the light intensity falls, are displaced downstream by the current, and so eventually reach the lake. In some instances spawning takes place below the outlet of a lake and the young fish are carried downstream until they reach a relatively quiet body of water. There they feed and grow, apparently become positively phototactic, and presently head into the current along the shores of the stream and enter the lake.

Chum salmon spawn for the most part in the lower sections of coastal streams. The young emerging from the gravel swim vigorously

into the current and tend to hold position. They prefer relatively bright light and when the light intensity falls they are displaced downstream and in due course reach the ocean.

The coho young, in contrast to chum salmon, do not go to sea immediately after emerging from the gravel but remain in the stream for a year. They are positively phototactic, but occupy territory along the margins of the stream and so escape displacement. In the following spring, radical changes take place in the behaviour of the yearlings as they transform from parr to smolt. These changes undoubtedly are associated with physiological changes. The fish lose their territorial behaviour and become negatively phototactic. When the light becomes weak, they rise in the water and so are displaced downstream.

The young sockeye enter the lake as fry and remain there until the following spring. As the water temperatures rise, the fish become very active and form into rapidly moving schools near the surface. They show a preference for currents and apparently move with the current as the temperature rises. As Hoar (1953) states, "osmotic stress, thyroid activity and increased rate of growth with extra demands for food are factors which may initiate restless appetitive behaviour and increase the general activity of the fish." Eventually they come under the influence of the outflowing water from the lake and are displaced seaward.

Several exceptions to the above-described cycle of events leading to seaward migration occur. Coho salmon may occasionally mature in resh water. Sockeye salmon frequently remain two years in a lake, and in northern waters may even remain three or four years before going to sea. Probably some of these delays in seaward migrations are the result of retarded development in cold water. Some may be more or less accidental. Foerster (1937) found at Cultus Lake that seaward migration ceased when the surface water temperature went above 15°C. approximately. Evidently the fish retreat from the warm surface water, called a "temperature blanket" by Ward (1932), and so fail to come under the influence of the outgoing current.

Some sockeye individuals, mostly males, remain in fresh water and mature at two, three, or four years of age. These have been designated "residuals" by Ricker (1938).

Finally there are populations of sockeye which are entirely fresh-water inhabitants. These are known as "land-locked" or "lake-locked" sockeye or "kokanees." Superficially at least, they are indistinguishable morphologically from sea-run sockeye but a critical study now being carried out by Mr. E. H. Vernon at the University of British Columbia may reveal distinctive characteristics.

Ricker (1940) has postulated that the kokanee has arisen from the

anadromous stock through genetic changes. If such be the case, it is evident that the genetic changes must have involved the endocrine system, since the behaviour pattern has been so altered that seaward migration no longer takes place. Segregation would have been established by kokanee spawning at times and in places distinct from the anadromous population. Systematists have accepted the idea of genotypic differences for some time in that they have recognized the kokanee as a subspecies, *O. nerka kennerlyi*.

Another possibility suggests itself, namely, that the kokanee exhibit reverse mutations and so represent, or are a near approach to, the very early freshwater stock of sockeye before the species became anadromous through genetic changes. In this case the sea-run fish are the original mutants.

However, it is possible that no significant genetic features are involved and that the differences between the anadromous, residual, and kokanee stocks are merely variants over a possible range from complete freshwater existence to complete anadronomy. The degree to which any portion of the range is developed may be associated with lake conditions, possibly largely with water temperatures. Some support to this idea is provided by the facts:

1. Anadromous, residual, and kokanee populations may all occupy a given lake.

2. The progeny of anadromous sockeye can be readily retained in fresh water. Ward (1932) described the occurrence of large numbers of sockeye maturing in Lake Shannon following the construction of a high dam on Baker River.

3. It is possible for kokanee to go to sea and mature there. Foerster (1947) marked and released a large number of kokanee yearlings below Cultus Lake and of these seventeen were subsequently taken as five-year-old fish in the commercial fishery.

4. Residuals and kokanee either do not occur in cold water lakes or occur only in very small numbers, so that their development may be associated with lake temperatures.

It would appear that a somewhat similar situation occurs with respect to the steelhead trout (*Salmo gairdneri*) and its freshwater forms, including the Kamloops trout and certain coastal stream populations.

Returning to the problems of migration, it is apparent that behaviour patterns associated with physiological and environmental conditions and changes account for the seaward movements of young Pacific salmon. The details of these interacting factors remain to be investigated.

Salmon juveniles entering the open sea will be carried northwestward

for a considerable period by the shoreward northwest currents. Their subsequent movements are possibly wanderings influenced by such ocean conditions as currents, temperatures, and food conditions.

As far as is known, the young fish remain over the continental shelf in the region between the northwest shore and the offshore southeast current. The early period of life in the ocean is one of vigorous feeding, fast growth, and accumulation of fat. In the second, third, or fourth summer, depending upon the species of salmon and the life history, it would seem that a series of endocrine activities on the part of the pituitary, thyroid, and gonads is initiated. At the same time, changes in the metabolic and osmoregulatory mechanisms take place. As a result of these profound physiological changes it is probable that the salmon exhibit an orthokinetic response whereby they tend to aggregate in water of lower salinity. At the same time they become positively rheotactic and swim into the current. These reactions will take them surfaceward, shoreward, and riverward and eventually upstream (Clemens, 1951).

The factors involved in the return to the home stream are not clearly understood but the investigations of Hasler and Wisby (1951) indicate that olfaction may be very significant, possibly on the basis of juvenile imprinting or conditioning.

The salmon proceed upstream until certain "sign stimuli" or "releasers" become effective and spawning takes place. The investigators in the field of ethology have provided a great deal of knowledge concerning the intimate dynamic relationships which exist between the organism and its environment (Tinbergen, 1951; Koch, 1942; Fabricius, 1950). The need for detailed knowledge concerning the behaviours and reactions of the species of salmon is becoming increasingly evident as stream and lake conditions are being changed through man's activities and as efforts are being made to maintain the salmon populations.

Information along the lines discussed in this section also has an important relation to transfers of salmon. Many attempts have been made to establish species of Pacific salmon in regions far removed from their native distributional area in the North Pacific. Perhaps the best summary is that of Davidson and Hutchinson (1938) who list the distributions of eggs and young of four species to the east coast of North America, to South America, to Europe, and to Australia and New Zealand. They point out that the only successful or temporarily successful transfers have been within the water temperature and salinity ranges of the native area, namely 3° to 18°C. approximately and a salinity probably not exceeding 34 parts per 1000. The only truly

successful transfer has been that of the spring salmon to the South Island of New Zealand. It may be that the coho or sockeye salmon has been established in southern Chile; Davidson and Hutchinson so record, but no confirmation has been obtained in recent years. Introductions of spring salmon into the Credit River, Ontario, and the St. John River, New Brunswick, and of pink salmon into streams of the State of Maine resulted in returns over several years but the stocks have now disappeared.

From what is now known of the rather intricate relations between the life cycles of the salmon and the environmental cycles, it is not surprising that failures in transfers have occurred. It seems clear that in any future considered attempt to introduce a species into a distant region many things should be taken into account—especially the coastal current systems, but also the ocean temperature and salinity ranges on the one hand and the behaviour patterns of the young of the species and freshwater environmental conditions on the other. Another feature will be mentioned later.

Metabolism

As indicated in the previous section, considerable changes take place in the metabolic activities of the salmon during the life cycle. Yearling sockeye in the early spring become very active and feed vigorously in rising water temperatures and in association with increased thyroid activity. In due course they reach the outlet of the lake and are displaced downstream to the ocean. During sea residence the fish feed vigorously on marine zooplankton, chiefly Crustacea, grow rapidly, and lay up fat reserves. With the approach of sexual maturity, feeding diminishes and finally ceases as the fish approach fresh water. The body reserves supply materials for the maturing of the gonads and for energy in swimming against the river current and for spawning activities. For some sockeye salmon of the Fraser River the stores must last for a month of vigorous swimming over a distance up to 700 miles at an average rate of about 27 miles per day, then for redd construction by the female and belligerent activity on the part of the male, and finally for the spawning act. Death ensues in the course of several days. Great differences exist among populations of sockeye in the distances travelled. For example, those proceeding to Cultus Lake go 100 miles and to an elevation of 190 feet. Those to Stuart Lake go approximately 700 miles and to an elevation of 2300 feet. Similar differences occur among the populations of the other species.

Most of our present knowledge of the metabolism of Pacific salmon is the result of the investigations on the spring salmon over a period

of some twenty years by Greene (1926). Additional fundamental information has been provided by Lovern (1934) and Fontaine (1951) on the metabolism of the Atlantic salmon. (Citation of all the papers of the above-mentioned three authors is considered unnecessary here.) Greene found that an adult spring salmon during its river migration lost 589 grams of protein and 1177 grams of fat from the muscles. During the migration period the ovaries may increase in weight by as much as 2000 grams. It is not pertinent here to review all the data which may have a bearing on the metabolism of salmon in relation to migration, but consideration of the metabolism is pertinent in relation to delays in migration and to the additional energy demands made by the imposition of fish-ways at high dams in the migration route. Excessive energy demands may result in the complete expenditure of the reserves before the fish are able to reach the spawning grounds or in the arrival of the salmon in such an exhausted state that spawning may be impaired or impossible. Knowledge of the metabolism is also important in relation to projects involving transplantations whether within river systems or to distant geographical areas.

It should be possible to determine the average potential energy of a fish of a given population and to calculate the rate of expenditure of the energy reserves in the stream at known temperatures and velocities. With this basic datum it should be possible to calculate the amount of surplus reserves available for delays or for mounting fish-ways.

The primary need is to recognize that the adult migrating salmon is a balanced mechanism adjusted to operate within a relatively stable cycle of environmental conditions and that changes interposed in the usual environmental sequence may disrupt the functioning of the animal mechanism.

Population Dynamics

By population dynamics is meant those fluctuating or cyclic changes which take place in the numbers of individuals constituting a population. Fishes which have more or less complex life histories, involving extensive movements between fresh and salt water and delicate interrelations with the environment, may be expected to have considerable fluctuations in numbers. This is the case among Pacific salmon, for sometimes a large influx of adults to a spawning area is followed by a small influx in the succeeding generation; conversely, a relatively small spawning population may produce a large return of adults of the next generation. The most critical analysis of fluctuating changes in abundance has been made by Neave (1952, 1953) who makes

certain modifications of ideas expressed by Solomon (1949). Only the freshwater portion of the life histories of pink and chum salmon are dealt with, for it is generally believed that fluctuations in abundance are predominantly of freshwater origin. Reference will be made briefly to the former species only.

Pink salmon mature invariably at two years of age. Therefore in any stream the two year-classes are completely distinct. No individuals of one year-class can breed with those of the other and there exists the phenomenon of two populations of a species utilizing a stream for reproduction but remaining as distinct as though occupying two completely isolated streams. The opportunity is presented therefore of comparing two populations within a very circumscribed environment. Neave shows that two populations frequenting a common stream fluctuate independently in numbers and that there is no evidence to suggest that the population of one year has any effect on that of the following. He states that population levels and changes are determined by three types of mortality. One is *compensatory*, in which mortalities become heavier as the population density increases or become lighter as the population density decreases. For example, the crowding of fish on the spawning beds will increase mortalities whereas the occurrence of fewer fish will decrease mortalities. The tendency thus should be for populations to "level off" and become stabilized, but this seldom if ever happens. Another type of mortality usually acts to prevent increase. In this type, known as *depensatory*, mortalities become relatively heavier as populations decrease in density. For example, predators in the stream existing at a fairly constant level of abundance will consume a larger percentage of fry from a small than from a large salmon population. Finally there is another mortality, *extrapensatory*, which is independent of population density. For example, a severe flood will affect a population irrespective of the density of the eggs in a stream bed. Extremely favourable water conditions may act in the opposite direction.

It appears, therefore, that extrapensatory mortalities tend to result in pronounced fluctuations in population size; that once a population is depressed it may be held there by depensatory mortalities until released by a change in extrapensatory mortality or until an important depensatory factor is eliminated. Such an analysis and classification of factors represents a fundamental approach to the problem of accounting for and measuring the significance of the various elements in a complex situation. Once the problem is clarified, it is possible to proceed with a logical series of investigations, the results from which may then be properly evaluated in the over-all picture.

Such a classification of ideas might well be used in studies of the fluctuations in abundance of all the species of salmon. In the case of the sockeye the problem is somewhat more difficult for, in addition to the corresponding incubation and fry migration periods, there is a year of lake residence followed by a more or less lengthy migration from lake to sea. Furthermore, there is the phenomenon of year-class dominance which exists among certain sockeye salmon populations but which may be merely a special phase of fluctuating abundance.

It is encouraging that increasing attention is being given to the discovery of biological principles in the biology of the Pacific salmon because the management problems in connection with the fisheries are of considerable complexity and their solutions require a broad background of knowledge. The genus *Oncorhynchus* constitutes a unique group for researches, the results from which will not only provide important contributions to knowledge but also lead to significant applications in the conservation of a very valuable fishery.

REFERENCES

BRETT, J. R. (1952). Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. J. Fish. Res. Bd. Canada, **9**: 265–323.

BROADHEAD, G. (1949). A study of the fecundity of the sockeye salmon (*Oncorhynchus nerka*) in the Chilko spawning area and a comparison with the sockeye salmon of the Cultus Lake spawning area. B.A. Thesis, University of British Columbia.

CLEMENS, W. A. (1935). The Pacific salmon in British Columbia waters. Rept. Comm. Fish. B.C., 103–5.

——— (1951). On the migration of Pacific salmon (*Oncorhynchus*). Trans. Roy. Soc. Can., 3rd ser., **45** (sec. V): 9–17.

DAVIDSON, F. A. and HUTCHINSON, S. J. (1938). The geographic distribution and environmental limitations of the Pacific salmon (genus *Oncorhynchus*). Bull. U.S. Bur. Fish., **48**: 667–92.

FABRICIUS, E. (1950). Heterogeneous stimulus summation in the release of spawning activities. Fish. Inst. Freshwater Res., Drottningholm, Rept., **31**: 57–99.

FOERSTER, R. E. and PRITCHARD, A. L. (1935). A study of the variation in certain meristic characters in the genus *Oncorhynchus* in British Columbia. Trans. Roy. Soc. Can., 3rd ser., **29** (sec. V): 85–95.

FOERSTER, R. E. (1935). Inter-specific cross-breeding of Pacific salmon. Trans. Roy. Soc. Can., 3rd ser., **29** (sec. V): 21–33.

——— (1947). Experiment to develop sea-run from land-locked sockeye salmon (*Oncorhynchus nerka kennerlyi*). J. Fish. Res. Bd. Canada, **7**: 88–93.

——— (1937). The relation of temperature to the seaward migration of young salmon (*Oncorhynchus nerka*). J. Biol. Bd. Canada, **3**: 421–38.

FONTAINE, M. (1951). Facteurs externes et internes régissant les migrations des poissons. Colloque Internat. Ecol., Ann. Biol., **27**: 569–80.

GREENE, C. W. (1926). The physiology of the spawning migration. Phys. Rev., **6**: 201–41.

HASLER, A. D. and WISBY, W. J. (1951). Discrimination of stream odors by fishes and its relation to parent stream behaviour. Amer. Nat., **85**: 223–38.

HAY, O. P. (1929). Second bibliography and catalogue of the fossil vertebrata of North America. Carnegie Inst. Wash., Pub. no. 390, **1**: 752.

HOAR, W. S. (1951). The behaviour of chum, pink and coho salmon in relation to their seaward migration. J. Fish. Res. Bd. Canada, **8**: 241–63.

——— (1951). Hormones in fish. Univ. Toronto Studies, Biol. ser., no. 59, Pub. Ont. Fish. Res. Lab., no. **71**: 1–51.

——— (1952). Thyroid function in some anadromous and landlocked teleosts. Trans. Roy. Soc. Can., ser. 3, **46** (sec. V): 39–53.

——— (1953). The behaviour of juvenile Pacific salmon with particular reference to the sockeye (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada, **11** (in press).

HOURSTON, W. R. (1949). The serological relationships of some Pacific coast Salmonoid fishes. M.A. thesis, University of British Columbia.

KOCH, H. J. (1942). Cause physiologique possible des migrations des animaux aquatiques. Ann. Soc. Roy. Zool. Belg., **73**: 57–62.

LOVERN, J. A. (1934). Fat metabolism in fishes. IV. Mobilisation of depot fat in the salmon. Biochem. J., **28**: 1955–60.

MACKINNON, D. and HOAR, W. S. (1953). Responses of coho and chum salmon fry to current. J. Fish. Res. Bd. Canada, **10**: 523–38.

MAKINO, S. (1937). Notes on the chromosomes of some teleost fishes. Zool. Mag., **49**: 75–6.

MILNE, D. J. (1948). The growth, morphology and relationship of the species of Pacific salmon and steelhead trout. Thesis, McGill University.

NEAVE, FERRIS (1952). "Even-year" and "odd-year" pink salmon populations. Trans. Roy. Soc. Can., 3rd ser., **46** (sec. V): 55–70.

——— (1953). Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Bd. Can., **9**: 450–91.

REGAN, C. T. (1914). Systematic arrangement of the fishes of the family Salmonidae. Ann. Mag. Nat. Hist., ser. 8, **13**: 405–8.

RICKER, WILLIAM E. (1938). "Residual" and kokanee salmon in Cultus Lake. J. Fish. Res. Bd. Canada, **4**: 192–218.

——— (1940). On the origin of kokanee, a fresh-water type of sockeye salmon. Trans. Roy. Soc. Can., 3rd ser., **34** (sec. V): 121–35.

SVÄRDSON, GUNNAR (1945). Chromosome studies on Salmonidae. Kungl. Lantbruksstyrelsen Medd. St. undersökn.-o. försöksanst. f. sötvattensfisket Nr. **23** (Rept. Swedish State Inst. Fresh-water Fishery Res. Drottningholm) Stockholm, 1–151.

SOLOMON, M. E. (1949). The natural control of animal populations. J. Animal Ecol., **1** : 1–35.

TCHERNAVIN, B. (1938). Notes on the chondrocranium and branchial skeleton of *Salmo*. Proc. Zool. Soc. London, ser. B, **108** (2): 347–64.

——— (1939). The origin of salmon: Is its ancestry marine or freshwater? Salmon and Trout Mag., no. 95: 120–40.

TINBERGEN, N. (1951). The study of instinct. Oxford University Press.

WARD, H. B. (1932). The origin of the landlocked habit in salmon. Proc. Nat. Acad. Sci., **18** : 569–80.

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA
VOLUME XLVII : SERIES III : JUNE, 1953
SECTION FIVE

FLAVELLE MEDALLIST'S ADDRESS

The Story of Listeria

E. G. D. MURRAY, F.R.S.C.

IN May, 1924, six cases of sudden death occurred in young rabbits in the animal breeding establishment of the Department of Pathology at Cambridge, with many more during the succeeding fifteen months. The interesting characters presented by the disease and the increasing mortality invited investigation. Although there seemed to be every reason to suppose the disease was an infection, the recognition of the agent proved troublesome, but by August a small gram-positive motile rod was isolated, which reproduced the disease characteristically in rabbits, guinea-pigs, and mice. By far the most striking character of this disease was the production of a large-mononuclear leucocytosis, and, as no similar micro-organism could be found in the literature, we called this new microbe *Bacterium monocytogenes*, in 1926.

Shortly before the detail of all this was published, Harvey Pirie discovered the same bacterium during August, 1925, in four wild gerbilles (*Tatera lobengulae*) in the course of his investigations of plague in South Africa, and, struck by the marked necrosis of the liver, he called the microbe *Listerella hepatolytica*, in 1927. It is a misfortune that the Rules of Nomenclature imposed on Pirie a need to change the generic name to *Listeria* in 1940, as the name *Listerella* had been used for a mycetozoon; and even the legitimacy of this later selection is in some doubt. Nevertheless, if I may be allowed the rhyme of the old name with that of a famous nursery heroine, I would like to tell *The Story of Listerella*, by analogy to the old fairy-tale, in which the unconsidered little girl became a personage of high importance.

I shall avoid entangling the main thread of the story with a recital of bacteriological, immunological, pathological, and clinical details, all of which are available to specialists in a quite profuse literature, because my present purpose is to bring out features of more general interest in the hope of intriguing the imagination by the wide biological rather than the narrow specialized aspects of the subject. I shall also disregard the chronological sequence, in order to group together

related interests with some measure of continuity, and integrate them with as much perspection as is possible.

A general interest in this disease is provoked by its wide geographic distribution and the surprising variety of host species in which it has been found. Serious epizootics in domestic animals give it a measure of economic importance and a number of sporadic human cases add to its significance. That it may yet prove to be one of the causes of the syndrome known as Infectious Mononucleosis in man is a controversial matter. In general it appears to have a low morbidity rate with a high mortality and its epidemiology and transmission are unknown, although a seasonal incidence and some relation to feeding and general hygiene have been noticed in domestic animals. The rarity of positive blood cultures is taken as an indication that transmission by blood-sucking arthropod vectors is unlikely.

So far as I know, *Listeria monocytogenes* has been isolated from natural disease in eighteen species of wild or domestic mammals and birds; in addition some others have been infected experimentally, and there are also the human cases reported from time to time. There is no reason to suppose the list is yet complete; it involves birds, rodents, ungulates, carnivores, and primates. Instances in these species have been found in nineteen different countries spread over every continent, and quite recently the interest in the disease seems to be increasing.

The form of the disease varies somewhat with the kind of host; it is predominantly a meningo-encephalitis in cattle, sheep, goats, and swine, and in some of these there is thought to be a preceding rhinitis; a metritis, with abortion, occurs in sheep, goats, swine, and cattle and the micro-organism has been found in the genital tract of rabbits, guinea-pigs, horses, cattle, and humans; in birds there is a marked myocarditis, which is also frequent in guinea-pigs; the disease is distemper-like in the fox; there is a conjunctivo-keratitis, which is quite peculiar, in rabbits, guinea-pigs, and horses; in many of these and in other animals it is a systemic infection marked by a necrotic hepatitis, but in the ferret it is a mild disease, almost a carrier state. In man many cases have been meningitis, some septicaemic; and a few cases in which *Listeria* has been isolated were clinically typical infectious mononucleosis. Quite evidently these various predispositions to host-selective lesions offer a special opportunity for the study of comparative pathology, since there is no essential difference in the strains of *Listeria monocytogenes* isolated from the varied conditions and different hosts. It has been suggested that this form of meningo-encephalitis might afford an experimental means of studying the

blood-brain barrier, especially since a marked angeitis of the smaller vessels of the brain has been observed.

A special form of the human disease has been described in Germany and called "granulomatosis infantiseptica" and it is interesting that one of the two human cases so far found in Canada conforms to this type. At least twenty-seven fatalities in newborn infants were found in Halle; these cases were generalized infections with extensive necrosis of the liver and *Listeria monocytogenes* was isolated from various organs. An identical *Listeria* was isolated from the vagina of the mothers, who remained well. This is interesting because of the metritis and abortion described in various kinds of domestic animals and the finding of *Listeria* in the genital tract of others, and, in addition, because in the original epizootic in the Cambridge rabbits the mortality was in the newly weaned baby rabbits, for the most part, and their mothers remained well. Even though sporadic cases occur in adult animals and human beings, these observations indicate a situation of peculiar interest and raise the general problem of age susceptibility to specific infections.

A finding with wider implications concerns twenty-four lemmings brought by Dr. T. H. Manning from Chesterfield and Morse Island in the Canadian Arctic to Ottawa, in the fall of 1949. Within a week of their arrival they were found to be dying of *Listeria monocytogenes* infection. It cannot be positively affirmed that they did not become infected on the way from Churchill to Ottawa, but it is interesting that another lot brought to Toronto more recently have the same disease. In no epizootic has listeriosis proved an exterminating disease; it has a relatively low incidence with a partiality for the immature and in the original Cambridge finding we noticed a definite relation to feeding in both incidence and recovery. The observations published on the Alaska 1949 cyclical mortality of lemmings describe tundra vegetation denuded by the lemmings without tangible indication of starvation. Rausch who made the Alaska report found "Dead lemmings were much in evidence, scattered over the bare tundra and surrounding snow." The greatest mortality was in juveniles. Convulsive movements in the dying were noticed and "there were no grossly visible lesions such as might be expected from bacterial infections," but the lemmings brought south and proved to have listeriosis frequently did not show gross lesions either. In the Alaska mortality the rapacity of owls, jaegers, foxes, and dogs for the dead and dying lemming could have regional possibilities, for birds and carnivores are susceptible and migrating raptorial birds might

conceivably carry infection. The cyclic decline in lemming population is not readily explained and the lemming is an important forage animal, so an infection that is not often easy to recognize and which could fit the case without much stretch of the imagination is worth a little suggestive speculation.

Almost exactly twenty years after publication of the description of the organism we found at Cambridge, a paper published in Sweden by Hulphers in 1911 came to light. In this he described an organism that is undoubtedly a *Listeria*, but I think probably a different species. Struck by the necrosis it produced in the liver he called it *Bacillus hepatis*. Pirie, too, was impressed by the hepatic necrosis caused by his Tiger River organism and called it *Listerella hepatolytica*. We, on the other hand, noticed in sections a remarkable infiltration of monocytes in the tissues and in the blood vessels, with massive oedema as well as the necrosis. These lesions might well predicate a toxin, and, like Hulphers and others since, we looked in vain for one. Thus the oedema and the necrosis have not been explained. However, since the astonishing monocyte response has been shown by Stanley to be evoked by a lipid of remarkable specificity, which is not only non-toxic but is not even antigenic, it becomes interesting to speculate whether profound pathological changes may not be produced by inherent substances or secretions of bacteria that are not toxins. But, bearing in mind the special conditions other bacteria require and the initial difficulties they presented, it may yet be that a toxin in the ordinarily accepted sense will be demonstrated for *Listeria*.

Another pathological manifestation in the natural disease is the profuse ascites and frequently pleural and pericardial effusions, which clot firmly in a test-tube. This fluid has not been examined biochemically, as far as I know, but it deserves to be because it contains a massive amount of triple-phosphate crystals. When viewed in a beam of strong light the crystals glint and give an appearance unusual to such exudates; they are so abundant that more than enough of them can be collected for chemical analysis by centrifuging ten to twenty cubic centimetres of exudate. This must indicate some peculiarity in disturbance of host metabolism and of bacterial character worth the knowing.

The mononucleosis characteristic of this disease very naturally attracted most attention and was quickly appreciated, judging by the immediate request for cultures. A monocytic reaction is somewhat characteristic of typhoid fever, tuberculosis, certain streptococcus infections, some protozoon diseases such as amoebic dysentery and trypanosomiasis, and at least one suspected virus disease, but its

genesis and function remain unexplained. Beyond saying that the etiology of the syndrome of infectious mononucleosis is still controversial and that an inference of a virus infection is justified in some cases, it is proper to note that *Listeria monocytogenes* has been isolated by different workers from typical cases and, with the support of indirect evidence, it seems possible that more than one cause exists.

Be that as it may, the mononucleosis caused by *Listeria monocytogenes* far exceeds that of any other instance. The circulating monocytes were shown by us to be increased by sublethal infection as much as 6,000 times, and it has been amply confirmed that this selective stimulation never failed to be produced beyond any need of statistical analysis to appreciate it. With it the absolute number of other blood leucocytes was but little disturbed.

The function, nature, and origin of the monocyte are still contentious and the fact that these cells are variously known as macrophages, monocytes, large-mononuclears, histiocytes, clasmatocytes, endothelial leucocytes, and plasmocytes shows an eclecticism indicative of uncertainty. The infection with *Listeria* affords a means of investigation far beyond the otherwise best limits of experimentally induced monocytosis, using tubercle bacilli or olive oil with Sudan III. Many have used *Listeria* with interesting results, but I shall not digress into the histological or cytological evidences produced to support the still varying views. Briefly, the prevailing view is that the monocyte, or certain of these diversified cells, are a transformation of the lymphocyte, though some maintain that there is a reticulo-endothelial hyperplasia or a specific monoblast. In any case, how and why the transformation occurs remain a mystery. There is no present understanding of the process inducing the monocytic response and the observation that ruminants do not produce a monocytosis, though susceptible to infection, has been neglected.

There still remains the all-important question of the function of the monocyte. It is not pre-eminently a phagocytic cell except in a very selective way. It takes up certain dyes peculiarly, it responds specially to lipid fractions of the tubercle bacillus to give histological features to the anatomical tubercle, and it takes up living tubercle bacilli in a moderate way. I have seen monocytes greedily ingest damaged neutrophyl leucocytes in exudates induced by the saliva of *Gastrophilus equi* larvae. Selective phagocytosis is not unusual, for even the familiar "polymorph" will take up carmine in preference to bacteria and one kind of bacterium in preference to another in a mixture. In the original investigations we showed that the monocytes produced by *Listeria* infection would cram themselves with living or dead *Listeria*, both

in vivo and *in vitro*, when they would refuse almost completely to ingest *Escherichia coli*. Selective phagocytosis is a much neglected subject but it is unlikely that this degree of activity can be the chief function of the monocyte.

The selective stimulation of a monocytic reaction by *Listeria* gained enormously in importance when Stanley discovered in 1949 that a chloroform-soluble lipid extracted from the bacterial cell was alone responsible for it. He also extracted the lipid from the liver of infected rabbits and could not find it in the normal liver. This lipid is not antigenic and is non-toxic, and produced a monocytosis of much the same order as the infection does, but of shorter duration, as might be expected. All this we confirmed extensively. At the time we were trying to produce a Paul-Bunnell agglutination of sheep erythrocytes with *Listeria*. We failed in this, but found that Stanley's lipid behaved as a weak Wassermann antigen. Thus we made an antigenic lipid-protein by precipitating the lipid with human syphilis serum. It is an interesting point, which confirms the specificity of the *Listeria* monocytosis, that some animals immunized with this lipid-protein complex developed a monocytopoenia coincident with production of antibody. The conditions and possibilities of this have not been pursued.

Stanley was quick to appreciate the potentiality of his lipid and showed before we did that animals with a monocytosis produced more antibody than did normal animals. There has been a great interest in Freund's "Adjuvants," using oils and tubercle bacilli to augment the production of immunity, some associating the effect with delayed absorption of antigen and neglecting the monocyte stimulation of these substances and what has been called "allergic irritability." At the same time, there has been a great interest in the origin and site of production of immune antibodies. Much has been done by blockading the reticulo-endothelial cells, by following the uptake of recognizable antigens by monocytic cells and its results, by investigating the concentration of antibodies at the prepared site of inoculation in comparison with that at a distance, by following the fate of lymphocytes with cortisone, and by extracting lymphocytes and macrophages to show their antibody content in response to immunization. Most of this inquiry is not much more than suggestive and there are divergencies in the interpretations.

We have added something to this information and part of the results are ready for publication while other interesting matter is still under investigation. We found it possible to maintain rabbits in a continuous state of high monocytosis by repeated injections of *Listeria* lipid and these rabbits produced four to eight times as much antibody as did

normal animals. We used three different types of antigen: whole typhoid bacilli, horse serum, and staphylococcus toxin, all with comparable success. As the lipid is not toxic and not antigenic, there is no interference with the health of the animals and the activity of the cells is not damaged, as they may be by some of the methods used by others. Pleural exudates were induced in immunized monocytosis animals and the washed cells, consisting of 98 per cent monocytes, yielded a higher concentration of antibody on extraction than was in the fluid of the exudate or in the circulating blood. We do not feel justified in concluding yet that antibody is made in the monocyte, because, when antibody from a normal rabbit is injected into a monocytysis rabbit, the collected monocytes contain a greater amount of the passive antibody than is present in the circulating blood. We have also shown that monocytes from a normal non-immune rabbit will take up a considerable quantity of antibody *in vitro*. Thus we do not know yet whether antibody is produced by other cells and the monocytes merely take it up and store it. It is quite evident that this approach opens vast possibilities in the investigation of immunity problems and the function of the monocyte.

There is implicit in these observations an explanation of the primary immediate disappearance from the circulating blood of passively introduced antibody. It raises the additional question whether this antibody stored in monocytes, which may account for the disappearance within twenty-four hours of at least 50 per cent of that introduced, might still be available for use, or might be destroyed in the cell. This is a matter of some importance in the serum treatment of disease and the answer could materially alter the applications of passive immunization. As yet I hardly dare speculate on the possibilities of influencing methods of active immunization, but in dreamy moments I see attractive hazy vistas only to be brought back to the realities limiting opportunity for experimental research.

This is an outline of the story of *Listerella*. Quite evidently a great part of it has been contributed by many workers whose names I have not quoted and a lot of varied detail of interest to specialists has been left out. "There is no man now on earth so artful in mind, nor so mighty in strength, that all these arts should be put upon him alone," and there is some merit in "le premier pas qui coute." It was my habit to keep complete notes of autopsies on all so-called normal animals which died, with bacteriological and histological examination of lesions. The noticing of apparently increased numbers of monocytes in the smaller blood-vessels in these sections is "the Glass Slipper" of this story.

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA
VOLUME XLVII : SERIES III : JUNE, 1953
SECTION FIVE

The Postglacial Pine Period*

PIERRE DANSEREAU, F.R.S.C.

POLLEN analysis shows rather a consistent dominance of pines in Eastern North America through a fairly considerable period of time. Potzger (1946) has assembled a number of pollen profiles that cover the Great Lakes area and they are consistent in revealing a well-defined pine dominance (see especially his figures 8, 9, 10, 11, 12, 14, 17, 22, 25). Allowing for the fact that species of *Pinus* are generally over-represented in pollen spectra, whereas some of their usual associates or near-associates (*Acer* and *Fagus* especially) are under-represented, it remains that pines in large numbers did occupy extensive areas for long periods of time.

In his general review of Pleistocene and postglacial biogeography, Deevey (1949) does not hestitate to characterize one of the three major subdivisions of postglacial time as a pine period (see his table 7). He emphasizes that "the resemblance to the European Boreal is too close to be ignored. Evidently in this interval the climate became considerably warmer and drier, and pines, presumably different species (e.g. *Pinus rigida* in New England, *P. banksiana* and *P. resinosa* in the Middle West), found suitable habitats on the poorer soils. It is not implied that pine forests occurred everywhere during this phase. The universal occurrence of large quantities of pine pollen (normally over 50 per cent) must mean that pines occupied at least the poorer soils while deciduous trees were still absent from the richer sites."

Deevey then goes on to contrast the striking regional differentiation during the following period, with the apparent uniformity of the pine period. However, he does not develop the interpretation quoted above and attempts no further description of the vegetation of the Boreal period.

More detailed study, such as that of Cain and his collaborators in southeastern Michigan (Cain, 1948; Cain and Cain, 1948; Cain, Cain, and Thomson, 1951; and Cain, unpublished), indicates the presence of at least three species of pine.

*Contribution no. 1003 from the Department of Botany, University of Michigan.

This forces us to face one of the most troublesome contradictions of plant geography: the fact that we must reconcile our extrapolation of present plant requirements into the past with our knowledge of evolutionary processes. It is hard to say which is more surprising, biologically speaking: the great stability (morphologically, at least) of some groups, such as *Gingko* and *Liriodendron* or the great change and multiform differentiation of others, such as *Nothofagus* and *Acer*. It is hard to decide upon, in fact vain to look for, any general rule concerning the balance of conservative and innovating forces within a phylum. There is evidence to show, at least on the infraspecific scale, that both processes are at work. It has been possible to detect them in the Californian closed-cone pines for instance, where there appears to be survival of unchanged old types together with appearance of new, modified ones—both of these phenomena (conservation and innovation) taking place within the changing matrix of the environment. (See Cain, 1944, chap. 9, pp. 104–21.)

If we add that physiological change may take place without any outward morphological sign, we can get ample confirmation from well-authenticated present-day instances: morphologically indistinguishable plants exist on different ploid levels and/or in different areas and/or habitats (Clausen, 1951). Such are the ways of evolution, detectable and undetectable, and of course, for the majority of plants, undetected.

May we then legitimately turn to a fossil flora and grade it by assigning indicator value to its components—reconstruct the vegetation itself by assuming that *Fagus grandifolia*, *Pinus*, *Lauraceae* indicate "cool-moist," "cool-dry," "tropical" conditions?

In the first place, it is rather evident, even from contemporary distributions, that the larger taxa offer the least reliable criteria. Genera are usable only if their ecological or bioclimatic limitations within a wide-ranging flora are quite sharp. For instance *Abies* is a better indicator in Eastern than in Western North America. As for species—when they can be positively identified!—their morphological stability may or may not be the outward sign of their physiological (and therefore ecological) stability.

Applying the above criteria to the postglacial pine period in Eastern North America, several explanations remain possible which are outlined below. Two principal hypotheses can be proposed. The first assumes that the three species of pine now widespread in glaciated eastern North America (*P. banksiana, resinosa, strobus*) had the same ecological requirements in the past as they have today. The second assumes that one or more of them did not have the same requirements.

Present Ecological Status of the Northeastern Pines

At this time, the jack, red, and white pines appear, ecologically, as a well-graded series consisting of three almost equidistant species in the order mentioned. From *banksiana* through *resinosa* to *strobus* the following requirements increase: moisture in air and soil (mostly the latter), humus content of soil, heat present in atmosphere (climatic, not necessarily edaphic). On the other hand, the light requirement decreases in the same order.

Much of the above has been demonstrated experimentally by Grasovsky (1929), Burns (1933), Shirley (1945), and many others, who confirm the relative positions of the three species along a light or a moisture gradient. Although they all require much light (at least in the earlier stages of their life-cycle) and can withstand various intensities of drought, it is also very apparent (a point which is much stressed by the above authors) that competition (especially in early stages of development) is ultimately the most important limiting factor. This latter point brings out the fact that in the foregoing paragraphs the term "requirement" has been used rather loosely. Ability to compete is hardly a thing-in-itself. It is the resultant of accumulated capacities, of successful adjustments, and varies a good deal in any and all species as they are exposed to different environmental conditions. Actually, the *ecological position* and the *potential ecological strategy* of the three species are only in part determined by their "requirements" in any strict sense of the word (Dansereau, 1952).

My principal concern here is the role played in natural communities by all three species: where they stand in relation to one another and in relation to other species of similar life-form and of neighbouring ecological status. It will turn out that each one shows certain requirements, tolerances, and capacities of utilizing the total resources of the environment. The various levels of efficiency attained will permit it to gain and to hold a certain ecological position in a habitat or general climatic environment that may be stable or changing.

Summarizing the ecological position of the three pines, it would seem to be generally agreed among ecologists and foresters who have wide field knowledge that they line up as follows.

Pinus banksiana (jack pine) ranges farthest north, into the subarctic taiga (lichen woodland), where it is sometimes a member of the prevailing open climax community, associated as a minor component with spruces; there, as well as in the south, it grows on rocky outcrops, mostly acid (granite, gneiss, quartzite), occasionally dolomitic ("lime-

stone pavement" of Manitoulin Island and Bruce Peninsula), and on sand plains. These sites are relatively dry and have little organic content. When the stand becomes at all dense, the species does not produce viable seedlings any more and one of the other pines, or spruce, or red maple sets in. Most remarkable is adaptation to fire: the jack pine's closed cones can survive a fire and the vast clearings that follow are favourable to its re-establishment notwithstanding the burning of humus at soil surface.

Pinus resinosa (red pine) is altogether the least successful of the three *at this time*. Its northern limits very nearly coincide with those of white pine and they are also very close to those of many ecologically important broadleaf trees (notably sugar maple). In fact the whole range of this species is within Nichols' (1935) "hemlock–white pine–northern hardwood" region and E. Lucy Braun's (1950) "beech–maple–hemlock" region. Red pine occurs on sandy and rocky (acid) substrate but not very often in extensive pure stands like the other two. For the most part it is associated with *P. banksiana* or *Populus tremuloides* on the drier and more open situations, and with *P. strobus*, *Acer rubrum*, or *Quercus rubra* on the more mesic sites. A canopy of about 50 per cent coverage seems fatal to its regeneration.

Pinus strobus (white pine) extends farther south than red pine, especially along the Appalachians at mid-altitude.[1] The moisture range of the sites it is found on is quite remarkable: from dry sand plains to the edges of bogs and arborvitae swamps. It seems to be absent from truly calcareous soils, whereas it does best on deep deposits of sand or not-too-coarse gravel. It is the only one of the three species which can achieve very dense pure populations of mature individuals. Under such conditions, although it is incapable of producing viable seedlings, it can maintain itself for very long periods of time. Although this is more in evidence in some areas than in others, it is generally agreed that white pine is not a climax dominant anywhere in Eastern North America at this time (Oosting, 1948).[2]

It thus appears that the three species are equipped for different functions, climatic and ecological. The white pine has the greatest ecological amplitude and is inserted into many different lines of succession (the bog hydrosere and the dune xerosere). The other two

[1]Outlying colonies have been reported in Mexican and Guatemalan highlands (Miranda and Sharp, 1950; Sharp, 1950).

[2]It is not argued that white pine is not an occasional or minor member of the maple–beech or maple–beech–hemlock climax community. But the view is taken here that extensive stands of pine were and are subclimax or at least edaphic and not climatic climaxes. Potzger (1946) has discussed this question in some detail.

are confined to the dry part of the ecological spectrum; and *P. resinosa* is further restricted to a rather narrow band within that.

Hypothesis I: Unchanged Requirements

If, in the course of the Pleistocene, the three pines acquired or had already acquired their present physiological adjustment to their environment, and had settled into their present ecological niches, they can be expected to have behaved during postglacial time as they do now. It will therefore be expected that their local abundance and association with other species will convey the same meaning as it does today in terms of both climatic and edaphic trends. If it can be shown that they did perform some function that they are now incapable of fulfilling, it follows that their (unchanged!) requirements found *another* adjustment to environmental conditions essentially different from any to which they are exposed today.

Under this present hypothesis of unchanged requirements four different situations (hereafter called cases A, B, C, and D) would explain the dominance of pine.

Case A: Long-drawn Succession

Whereas during ice advances the cliseral movement proceeded through the contamination and eventual replacement of communities by other communities of equal seral status (climax by climax, serclimax by serclimax, pioneer by pioneer), during ice retreats progression over newly liberated areas, although uneven in rate, largely proceeded through occupancy by many seral stages, at least on the "better" sites.[3] In other words, while the southward movement allowed a community with high requirements to move directly onto a highly differentiated soil (spruce–fir moving into beech–maple), it was necessary for that same community on its way back north, to have other communities before it build up the soil, unless, indeed it could do so itself.

Many questions arise in this connection which can only be hinted at for the moment: How well can biological replacement of beech–maple by spruce–fir keep up with the pace of a "deteriorating" climate? How soon can the replacement of spruce–fir by beech–maple catch up with climatic "improvement"? There would always seem to be a lag: survival of relict deciduous forest during the ice advance; slowness of edaphic build-up during the ice retreat. If this latter were extremely prolonged, true climatic control would not set in

[3]E. L. Braun (1950) refers to the well-drained upland as "average" topography.

(at least not in a general way and over most of the area) within the duration of the climatic cycle itself. Braun (1950, 1951) believes that there is evidence even today that many Tertiary species, disturbed by glaciation, have not yet regained their former positions and are at this time checked in their expansion not so much by climate as by the relative immaturity of soils. Obviously this line of reasoning can be applied only to climax or near-climax species.[4]

In Case A, then, *pine dominance* (most likely white pine) *is explainable in terms of a prolonged succession which never attained its* (deciduous?) *climax status*, and *the apparent boreal pine climax is in reality a long-enduring subclimax.*

The persistence of vast areas of white pine to this day and the readiness with which they are supplanted by broadleaved trees when released by lumbering fit this case quite well.

Case B: Dry-Cold Climate

If there is postulated a former climate which was approximately that of the Great Lakes today in temperature fluctuations, whereas the total precipitation is assumed to have been much less, then no area in the East duplicates such conditions today. In fact, as long as much ice still plugged the Great Lakes themselves, it is not unreasonable to suppose more pronounced continentality in the climate. Whereas today there is practically no climatic savana (or woodland) between the grassland and the forest in Eastern North America, it is by no means unusual for such an intermediate formation to occur. Pine savana is almost constantly present in Western North America where desert, grassland, or steppe abuts onto the forest, whether the latter be broadleaved or needle-leaved. It makes a considerable difference in our interpretation if we do not accept "pine" as necessarily indicative of "forest," but recognize its potential role as a savana tree. Of the three being considered here, it seems that *P. banksiana* is indeed exactly that in the Canadian taiga, where, however, it is of minor importance as a true climax species. Throughout its range, whatever its successional status, it is most often a member of an open savana or park-like formation. *P. resinosa* is perhaps even more markedly a savana tree.[5] It is worth pointing to the role played by the closest relatives of these two species. *P. contorta* and its many

[4]That is to say, to those that are obligate mesophytes and not to those which persist in climax, but become established earlier and thereby show some independence of degree of maturity of the soil.

[5]I have discussed the importance of structure in vegetation and attempted to outline its significance and variations at some length in another paper (Dansereau, 1951).

segregates in Western North America (including *P. murrayana* characteristic of the "Hudsonian" belt in the Sierras) are very much like *P. banksiana* and quite frequently grow in very open stands. Even more striking is *P. ponderosa*, in many ways very similar to *P. resinosa*, which on the western edge of the Great Plains seems to offer a picture of the *P. resinosa* savana or savana woodland that could very well have bordered the Great Lakes in postglacial times.

In Case B, *low precipitation induced a climax savana formation of jack or red pine.* It is entirely possible that increased heat without proportionately increased precipitation resulted in a shift from the dominance of jack to red pine without much change in vegetation structure.

Case C: Greater Illumination

Low light intensity at forest floor level seems to be primarily responsible for failure of white pine to maintain itself, whether under its own shade or that of other species, needle-leaved or broadleaved. Amount of light in the forest is of course a function of amount of radiation that penetrates through the atmosphere. At the present time the mean cloudiness in the Great Lakes is quite high (Brooks, Connor, *et al.*, 1936). Table I permits a comparison with other parts of North America. It will be seen that light availability is highest in the Sierra Nevada where the most truly mesophytic and most shade-tolerant of

TABLE I

MEAN CLOUDINESS IN VARIOUS AREAS, WHERE PINES ARE OF ECOLOGICAL IMPORTANCE

(Brooks, Connor, *et al.*, 1936)

Region	Southern Appalachians	St. Lawrence	Great Lakes	Colorado	Sierra Nevada
Pinus spp.	*virginiana* *echinata* *taeda* *rigida* *strobus*	*banksiana* *resinosa* *strobus*		*contorta* *ponderosa* *flexilis*	*contorta* *ponderosa* *flexilis* *lambertiana* *monophylla*
Mean cloudiness January	6–7	6–7	6–8	5–6	4–6
July	5	5–6	4–5	4	1–2

all American pines is found: *Pinus lambertiana*, the sugar pine, is an authentic forest climax species. It also is a close relative of the eastern white pine.

Case C, then, offers the possibility that the intolerance of *Pinus strobus* could have been overcome in the past if greater illumination had prevailed.

Case D: Higher Climatic Anomalies

Today the Great Lakes area, as compared with the Central Plains, shows relatively equable conditions. The North American maximum range of temperatures (46°C. and more in Brooks, Connor, *et al.*, 1936) lies in the Mackenzie district roughly between 55° and 65° Lat. N and 95° and 125° Long. W. This trend is gradually and almost regularly attenuated to the southeast on the axis of 100° Long. W where the range of 24–30° lies between 35° and 42° Lat. N. This same range (24–30°) is then oriented in a northeasterly direction on an axis perpendicular to the Great Lakes–St. Lawrence between 42° and 48° in the western Great Lakes and 50° and 55° in Newfoundland and Labrador. The middle and upper St. Lawrence, however, have 30–32° ranges. This latter is the result of a thrust from the Mackenzie centre[6] which is quite analogous to the southward push along the 100th meridian.

I venture to suggest that in postglacial times these anomaly lines were displaced and that the bulge which surrounds the Great Lakes must not have existed at all for quite some time posterior to deglaciation. It is therefore entirely possible that the high anomalies that dominate the taiga may have existed at more southerly latitudes where they need not have involved mean minima very much lower than those which prevail today. Such large-scale fluctuations, which may well have also been irregular, can be thought of as offering a background to plant succession, such as does not exist today, at least on the same scale, in the Great Lakes region. What might have been involved is a state of flux between the conditions essentially favourable to the hardwoods and those essentially favourable to spruce–fir. Whereas the white pine community is now subclimax to hardwoods, and occasionally (as in the Gaspé Peninsula and northern Ontario) to spruce–fir, it may possibly have held its own in an area that was alternately favourable to the one and to the other and never for very long to either one.

[6]Hare and Montgomery (1949) have shown how the winters of the Hudson Bay are truly continental as a result of frozen water and oppose no resistance to the above-mentioned movement.

Case D *supposes* Pinus strobus *to have been climax in areas of long-continued climatic variability or of rapidly alternating periods of different climates.* The intricate patterns of individual climatic factors and the sharp gradients that they reveal in the central lower peninsula of Michigan and the plateaus of Pennsylvania suggest a possible relation of white pine stands (primevally well developed there) to climatic instability.

The Shifting Order of Past and Present Vegetation

If one postulates that the three pines we know today are descended from ancestors that may or may not have been morphologically identical to them but were somewhat physiologically (and therefore ecologically) different, it would amost seem that there are endless possibilities.

This will hardly be so, however, in any one line of descent, as it is unsafe to assume too much or too many changes. Palynological data themselves provide us, after all, with a generally coherent picture of plants in the past that are associated with the same other plants with which they grow today: the beech and maple are commonly found together, so are the birches and alders, so are the oaks and chestnuts, the spruce and fir.[7] An over-all view of fossil pollen aggregates rather points to a certain cohesion of the phytosociological units which can only be due to a compatibility founded on both similar and complementary requirements. In the light of this interpretation, Hypothesis I answers the principal questions raised by the position and relative abundance of the pines.

It is, however, permissible to consider the possibility of evolution of the modern pines from ancestors that differed from them in some respect, although this divergence cannot be postulated to involve any one or all possible ecological functions. Our best estimate of the kind, degree, and direction of deviation which modern pines underwent in postglacial times can be made on the basis of their previous history. This approach has already been implicitly suggested above when a comparison was made between *P. strobus* and *P. lambertiana*, and between the other eastern pines and their western vicariants. A further step would consist in reconstructing as accurately as possible the Pliocene environment and in working back in the Tertiary and

[7]This in itself is hardly conclusive since we cannot be sure of the time at which dominance was achieved by one or more species. At the time of the rise of the Angiosperms, various species of *Fagus*, *Nothofagus*, *Quercus*, *Acer*, etc., displaced entirely or in part the reigning *Podocarpus*, *Tsuga*, *Pinus*, etc., and there must have been later shifts among the Angiosperms themselves.

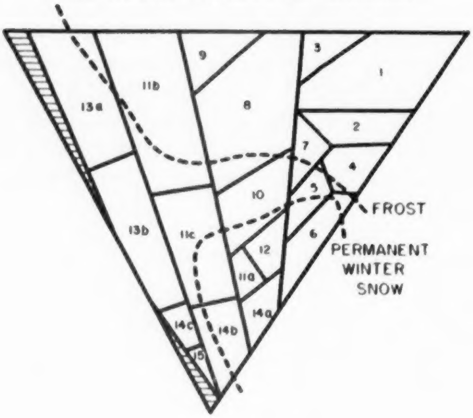


FIGURE 1. A world scheme of correlation of plant formations and major climatic influences (modified from Dansereau, 1951, Fig. 5). Extreme of warmth and moisture is in upper right-hand angle, extreme of warmth and drought, upper left-hand angle; extreme cold and low precipitation, lower angle. The figures in the divisions refer to Schimper and von Faber's (1935) formation types, as follows (examples in parentheses):

1, Tropical rain forest (Amazon). 2, Subtropical rain forest (New South Wales). 3, Monsoon forest (Burma). 4, Temperate rain forest and cloud forest (New Zealand). 5, Summergreen deciduous forest (Eastern North America). 6, Needle-leaf evergreen forest (northern Ontario). 7, Evergreen hardwood forest (southern France). 8, Savana woodland (northeastern California). 9, Thorn forest and scrub (northeastern Brazil). 10, Savana (central Brazil). 11a, Scrub steppe (Wyoming). 11b, Steppe (S. Dakota). 11c, Prairie (Iowa). 12, Heath. 13a, Dry hot desert (Sonora). 13b, Dry warm desert (Mojave). 14a, Cold woodland (Labrador hinterland). 14b, Grassy tundra (Seward Peninsula). 14c, Rocky tundra (N. Baffin). 15, Cold desert (N. Greenland). Horizontally striped areas have no vegetation. The approximate limits of frost and of permanent winter snow are shown.

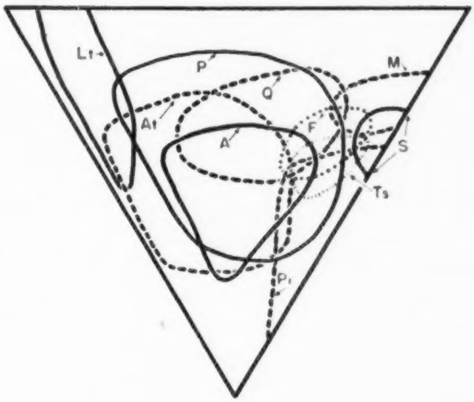


FIGURE 2. Superimposed upon Fig. 1 are the approximate limits of several genera or smaller taxa, with which the present discussion is concerned. Their distribution in North America is outlined with respect to the major formations which they span. They are as follows:

A —*Andropogon gerardi*	P —*Pinus*
At—*Artemisia tridentata*	Pi—*Picea*
F —*Fagus*	Q —*Quercus*
Lt—*Larrea tridentata*	S —*Sequoia*
M—*Magnolia*	Ts—*Tsuga*

Mesozoic to the initial contest between the needle-leaved evergreen conifers and the broadleaved deciduous Dicotyledons.

We can view some of the highlights of the evolutionary sequences, the morphological transformations, the geographic isolations that took place in that long period. It is possible to follow the development of certain phyla—and even genera—quite well, but difficult to reconstruct the entire plant communities, the whole vegetation matrix that served as a very real background (with all its accumulated and cumulative pressures), to evolutionary processes.

No documented synthesis of the vegetation of North America in pre-Pleistocene times is available, although many regional studies have been made. However, the floristic character and climatic limitations of some of the important vegetation units are known and a scheme showing the order of replacement of the one by the other can be devised. Also some estimate is possible of the shifts in requirements that enabled certain species to become dominants and thereafter to maintain or lose that position.

This relationship is pointed up in Figs. 1 and 2. Fig. 1 (somewhat modified from Dansereau, 1951) shows a world scheme of the principal climatic vegetation types and Fig. 2 shows the range of certain plant groups with which the present discussion is concerned through two or more formations.

The principal vegetation units involved in the North American late Tertiary, Pleistocene, and Recent are the following: (1) *temperate rain forest* (and its montane equivalent, cloud forest); (2) *redwood forest* (also a modified temperate rain forest); (3) *hemlock–cedar forest* (a further attenuation of the rain forest complex); (4) *deciduous* or *summergreen forest*; (5) *needle-leaved forest*; (6) *oak-openings* (a savana woodland); (7) *pine woodlands*; (8) *sagebrush*; (9) *creosote bush*; (10) *grassland*.

These ten types will not be described here. They are well outlined in Shantz and Zon (1924), while the major vegetation-types to which they belong are described and justified in Schimper and von Faber (1935). Our interest lies in their points of contact and their potential for moving along a climatic gradient in a certain order. Table II shows four sequences, each involving three stages of replacement under changing climates.

It will be seen in both Fig. 1 and Table II that *Pinus* not only occupies a central position but also ranges more widely than any of the others. Considering, then, the present position of pines, their occurrence at various levels in pollen diagrams and their occasional dominance; considering also the origin of the regional formations

within which they grow or by which they are eventually displaced, what can be construed concerning their past requirements if the latter are assumed to have been any different from their present ones?

TABLE II

SOME OF THE PRINCIPAL CLISERAL ALIGNMENTS IN NORTH AMERICA AT THE PRESENT TIME

Magnolia (warm-moist)	*Fagus* (cooler)	*Tsuga* (cooler)	*Pinus* (cool-dry)
Sequoia (warm-moist)	*Quercus* (drier)	*Pinus* (cooler)	*Artemisia* (cold-dry)
Larrea (hot-dry)	*Artemisia* (cooler)	*Pinus* (moister)	*Picea* (cold-moist)
Artemisia (cold-dry)	*Andropogon* (moister)	*Pinus* (moister-colder)	*Picea* (cold-moist)

HYPOTHESIS II: CHANGED REQUIREMENTS

Three cases are outlined below, if ***Pinus banksiana*** and/or ***P. resinosa*** and/or *P. strobus* emerged from the Pliocene with sensibly different genetic make-ups than those which they now possess. Whereas, under Hypothesis I, genetic identity was assumed and exposure to presently non-existing environment was postulated, under Hypothesis II genetic difference is assumed and an explanation will be sought primarily in terms of exposure to presently existing and familiar environmental conditions. It will be obvious that *differences in both heredity and environment* will necessarily have existed at some time in the development of each one of the taxa concerned. For greater convenience the ancestors of the three northeastern pines will be called *P.* "prebanksiana," *P.* "preresinosa," and *P.* "prestrobus," as the assumed differences potentially have specific importance whether or not they were accompanied by morphologically visible features.

Case E: Greater Shade Tolerance

Pinus "prestrobus," having diverged less from *P. lambertiana* or other more equable-climate species from which it was derived,[8] was able to reproduce in the shade. If the analogy with *P. lambertiana* has any value, however, and if the latter has retained more of the ancestral qualities of the stroboid line of descent, because it has been

[8]Or indeed to which it gave rise!

exposed more constantly to equable conditions, it will be noted, on the other hand, that it does not achieve greater abundance. This, however, is in part a function of the degree to which its responses (requirements and tolerances) overlap those of its associates (*Pinus ponderosa*, *Pseudotsuga taxifolia*, *Abies concolor*, *Acer macrophyllum*, and, locally, *Sequoia gigantea*). Essentially *P.* "prestrobus" was facing a different situation, its competitors, with the exception of hemlock, being broadleaved-deciduous. Shade tolerance here may not have been enough as these others have an entirely different (and more advantageous?) seasonal rhythm; their root system, the physico-chemical nature of the litter they produce, and the soil profile which they eventually initiate could all combine to outweigh an equality of response to the light factor. It would seem fairly clear in this respect that *Tsuga canadensis* (which is admittedly also very shade-tolerant, in fact quite as much as or more so than the hardwoods) is less at a disadvantage because of these other factors than *Pinus strobus*.

Case F: Greater Drought Tolerance

Pinus "preresinosa" in order to maintain its dominance would have had, like *P. prestrobus*, to be more tolerant of shade. Barring this, however, it could have been dominant (as suggested in Case B) if the climate had been favourable not to closed forest, but to savana or woodland. This is the situation under which *P. ponderosa*, its relative,[9] operates most successfully. Therefore, if it had been somewhat more drought-resistant, *P.* "preresinosa" could have held its own.

P. resinosa is now, of course, well adapted to edaphic drought, in fact it occurs on flat Potsdam sandstone slabs and on overdrained sandy hills. It is however almost wholly confined to areas of more than 30 inches of annual rainfall and less than 20°C. mean July temperature. Its western counterpart shows no such narrowness: its lower limit is very nearly 20 inches of annúal rainfall whereás its minimum temperature requirements are close to 23°C. July mean temperature (Stage, 1952).

Case G: Greater Moisture Tolerance

Compared to their vicariants, *P. contorta* in western North America and *P. sylvestris* in Europe, the jack pines of eastern North America are singularly depauperate. Two species are known: *P. virginiana* now almost entirely south of the glacial border and *P. banksiana* entirely

[9]The relationships of the pines are now being tested by breeding (Heimburger) and by chemical determination of their resins (Mirov) and some unexpected affinities are being revealed.

north of it. They do not come in contact anywhere. Neither is variable to any extent, certainly in no measure comparable to the other two mentioned above. Moreover, the amplitudes of both of the former are tremendous. Climatically they range from the mild maritime conditions of the Pacific Coast and the Baltic to the subalpine heights of the Sierras and the Alps. Ecologically they occur in the bogs of Oregon and California at various altitudes to the bare granite domes of the Sierra Nevada and from the moors of Scotland to the dry valley floors of the upper Rhone in Switzerland. Quite apart from being present at both ends of the ecological spectrum (hydrosere and xerosere), in many parts of Europe and Western North America these pines actually form forests. It is true that these are not often of great density but they are nevertheless forests and not woods, parks, or savanas.

It is easy to see how this same pattern may once have prevailed in ***Pinus*** "prebanksiana" and how it might, in such a case, have achieved and maintained dominance.

Conclusions

The foregoing pages raise more questions than can be answered at this time. They also accumulate so many suppositions that speculation far outweighs the concrete evidence, and implications are more numerous than conclusions. In an attempt to evaluate a palynological problem, it has been necessary to question all existing interpretations and also to restate some general principles of both ecology and plant geography which do not have a satisfactory grounding at this time.

The basic contradiction which taints much floristic and bioclimatic investigation is here brought into the open. The seven cases discussed under the two hypotheses are probably not the only alternatives that would satisfactorily explain the pine period.[10] I hope that others will be proposed. Nor do I think that they are mutually exclusive. It is more likely that, when we have learned more concerning some of the details and arguments mentioned here, some combination of these cases will provide the most satisfactory explanation.

[10]No mention was made of *Pinus rigida*, *P. echinata*, and *P. virginiana*, all of which slightly overlap in area with *P. strobus* and whose cliseral movements may have involved them in the "pine period." Their climatic (not edaphic) moisture requirements seem to be very high. But they too, of course, could have had different requirements in the past.

REFERENCES

Braun, E. Lucy (1950). Deciduous forests of Eastern North America. Philadelphia, Toronto: Blakiston.

BRAUN, E. LUCY (1951). Plant distribution in relation to the glacial boundary. Ohio J. Sci., **51**: 139–46.

BROOKS, C. F., CONNOR, A. J. *et al.* (1936). Climatic maps of North America. Cambridge: Harvard University Press.

BURNS, G. P. (1933). A study of natural reproduction in Vermont forests. II. The effect of thinning on white pine reproduction. Vt. Agr. Exp. Stat. Bull., **354**: 1–24.

CAIN, STANLEY A. (1944). Foundations of plant geography. New York: Harper.

——— Pollen profile of a lake in the Edwin S. George Reserve, Mich. Unpublished.

——— (1948). Palynological studies at Sodon Lake. I. Size-frequency study of fossil spruce pollen. Science, **108** (2796): 115–7.

CAIN, STANLEY A. and CAIN, LOUISE G. (1948). Palynological studies at Sodon Lake. II. Size-frequency studies of pine pollen, fossil and modern. Amer. J. Bot., **35** (9): 583–91.

CAIN, STANLEY A., CAIN, LOUISE G., and THOMSON, G. (1951). Fossil pine pollen size-frequencies in Heart Lake sediments, Oakland County Michigan. Amer. J. Bot., **38**: 724–31.

CLAUSEN, JENS (1951). Stages in the evolution of plant species. Cornell University Press.

DANSEREAU, PIERRE (1951). Description and recording of vegetation upon a structural basis. Ecology, **32** (2): 172–229.

——— (1952). The varieties of evolutionary opportunity. Rev. Can. Biol., **11** (2): 305–88.

DEEVEY, E. S., JR. (1949). Biogeography of the Pleistocene. Bull. Geol. Soc. Amer., **60**: 1315–416.

GRASOVSKY, A. (1929). Some aspects of light in the forest. Yale Univ. Sch. For. Bull., **23**: 1–53.

HARE, F. K. and MONTGOMERY, M. R. (1949). Ice, open water and winter climate in the Eastern Arctic of North America. Part I (F. K. HARE). Distribution of winter temperature over the Eastern Arctic and Sub-Arctic. Arctic, **2**: 79–89.

MIRANDA, F. and SHARP, A. J. (1950). Characteristics of the vegetation in certain temperate regions of eastern Mexico. Ecology, **31** (3): 313–33.

NICHOLS, G. E. (1935). The hemlock–white pine–northern hardwood region of Eastern North America. Ecology, **16**: 403–22.

OOSTING, HENRY J. (1948). The study of plant communities. San Francisco: Freeman.

POTZGER, J. E. (1946). Phytosociology of the primeval forest in central-northern Wisconsin and upper Michigan, and a brief post-glacial history of the Lake Forest formation. Ecol. Monogr., **16**: 211–50.

SCHIMPER, A. F. W. and VON FABER, F. C. (1935). Pflanzengeographie auf physiologischer Grundlage. Two vols. Jena: Fischer.

SHANTZ, H. L. and ZON, R. (1924). Natural vegetation. *In* Atlas of American agriculture. U.S. Dept. Agr.

SHARP, A. J. (1950). The relation of the Eocene Wilcox flora to some modern floras. Evolution, **5** (1): 1–5.

SHIRLEY, H. L. (1945). Reproduction of upland conifers in the Lake States as affected by root competition and light. Amer. Midl. Nat., **33**: 537–612.

STAGE, ALBERT R. (1952). Growth determinants of ponderosa pine. Unpublished term paper, Department of Botany, University of Michigan.

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA
VOLUME XLVII : SERIES III : JUNE, 1953
SECTION FIVE

Life's Progressive Orderliness based on the Binary Statistic of Genic Alleles

A. H. HUTCHINSON, F.R.S.C.

THE eminent physicist Erwin Schrödinger in his series of lectures on *What is Life?* presented at Dublin and published by the Cambridge University Press (1951) states: "The unfolding of events in the life cycle of an organism exhibits an admirable regularity and orderliness, unrivalled by anything we meet in inanimate matter. We find it controlled by a supremely well ordered group of atoms (the gene). Moreover we conclude that the dislocation of just a few atoms within a group of governing atoms of the germ cell suffices to bring about a well defined change (or mutation) in the large scale hereditary characteristics of the organism." "In the light of our present knowledge the mechanism of heredity is closely related to, nay founded upon, the very basis of the quantum theory." "It now seems to be possible to point out in a more direct manner the connection between quantum jumps and mutations." "These facts are easily the most interesting that science has revealed in our day . . . an organism's astonishing gift of concentrating a stream of order on itself and thus escaping the decay into atomic chaos—of drinking orderliness from a suitable environment."

The binary basis of biotic order and continuity. Life's continuity is not that of a smoothly flowing or otherwise turbulent stream; it is the quantisized continuity of the shuttle in the loom or in the badminton game which alternates between two poles; the reversible reactions are dependent upon the reciprocal action of opposite forces or co-actors. Again, life's continuity is frequently attained by the cyclic principle of the wheel or spiral where the "quantum jumps" of "to and fro" are smoothed but none the less real. To illustrate: the interaction of male and female reciprocals; the sperm and egg; the homologous chromosomes; the allelic genes; the cyclic alternation of x and $2x$ generations including the reciprocal processes of syngamy and meiosis resulting in the segregation and recombination of genic units. Recent investigations give examples of life's binary phases and alternations in the lowly unicellular algae, yeasts, and bacteria. These are life principles.

The segregation of genes at meiosis is not random; one gene from each allelic pair goes to either of two poles. If chance were in charge there would be an infinite number of poles and any number of like or unlike genes could go in any direction. The number of possibilities of combinations of genes, one from each pair at one of two poles, to form new gametes is quantisized and the distribution is orderly. This orderliness results in definite integral allotments of genotypes. If the hybrids of the first filial generation are heterozygous for n genes, 2^n kinds of gametes are produced, 3^n kinds of genotypes are formed, and 4^n is the least number which makes possible all recombinations. The integral proportions of the genotypes are not fractional; they are specifically 1, 2^1, 2^2, 2^3, 2^4, 2^n where 1, 2, 3, 4, n represent the number of heterozygous alleles involved. The system is one of quantisized orderliness.

Order from order. The orderliness of life processes and products stems from the orderliness of the gene, which is composed essentially of nucleic acid. The orderly configuration of four groups of PO_4; four cyclic five-carbon sugars (ribose); two single-ring nitrogen-containing pyrimidines, and two double-ring purines form the base of the nucleic acid polymer. It is notable that three of these units, adenine, ribose, and phosphate, enter the molecule of A.T.P. adenosine triphosphate, the high-energy compound which facilitates the synthesis of food (Stumpf, 1953). The definite locus of each allelic gene has further significance, known as "the position effect," evident in the phenotypic expression and relative distribution of genes. Again to quote Schrödinger (1951): "Whether we find it astonishing or whether we find it quite plausible that a small but highly organized group of atoms be capable of acting in this manner, the situation is quite unprecedented, it is unknown anywhere except in living matter." Genes are specific in their direction of the final composition of the important protein molecule.

Comparison of the genic orderliness with "chance" occurrences. The odds against holding any specified hand of cards, for instance 13 spades, are 635, 013, 559, 559 to 1. On the contrary the repetition of the Hapsburg lip has continued in regular sequence for centuries and Marquis wheat has repeated itself without failure trillions of times. If the same "chance laws" of distribution within the nucleoprotein of the gene were to hold sway, the several thousand atoms would have a variability such that repetition could not be expected within the time period of the planets. There would be no species of organisms—nothing but a cosmos of freaks.

Mutation, a quantisized genic change. Recent investigation, particularly on the nutrition of Neurospora (Beadle, 1945), demonstrates that gene mutations are not random and in all directions. On the contrary they are in series, step-wise, and limited in degree; there is a gene for each enzyme and consequently for each step in the metabolic process. In addition, the well-known feature holds that mutation is reversible and the rate in either direction is specific, under constant conditions. Change of conditions, such as treatment with X-ray or with colchicine, gives a general increase or decrease in rate but does not affect the relative rates. Survival values may be changed, however. In each case there is regularity, orderliness accompanied by flexibility and selection.

Automatic control and feed back. Recently automatic control and "feed back" have become "conspicuous and widely felt in the mechanics of today"; in thermostats and electric clocks for instance. To quote from Ernest Nagel (1952): "Every operating system from a pump to a primate exhibits a characteristic pattern of behavior and requires a supply of energy and a favorable environment for its continued operation." Further reference to the genic control of the energy releasing A.T.P. may suffice to emphasize the universality of basic "automatic" control in organisms. Consider the energy expenditure of a humming bird in flight and as it hangs pendent at night—a self-adjusting, "automatically" regulating control which is specific to humming birds and varies in rate from one to twenty times the basal rate.

Orderliness versus chance. "The solar system shows so many regularities both in its dynamical and its physical properties that it cannot have been formed by chance. La Place estimated that the odds against these regularities being due to chance was more than 2×10^{-14} to 1" (Jones, 1951). "In the formation of crystals the chances of a nucleus of critical size being formed by random motions of molecules on the surface . . . if expressed as a decimal turns out to have a thousand noughts between the decimal point and the first digit different from nought for a supersaturation of one per cent" (Burton, 1951). What then is the probability that random forces may account for the formation of desoxyribonucleic-acid crystals and for their specific activities? It is estimated that the age of the universe does not give sufficient time for the origin, growth, and repeated reproduction of a single mammal species by chance.

The statistic of the gene. Schrödinger speaks of "our beautiful statistical theory of which we were so justly proud because it allowed us to look behind the curtain to watch the magnificent order of exact

physical law coming forth from molecular disorder." Biologists and others, following the mathematician, have utilized the infinity extension of the binomial law in attempts to explain the "normal distribution" of population classes: attempts have been made to study the genetics of human populations without reference to ancestry; the best that can be expected for any individual is an approach to the law of random distribution within the limits of standard deviation; the best that can be attained is to shift the population mean by mass selection, without permanence. Real progress has resulted from recognition of the genes as quantisized units giving origin to particular genotypes. DeVries, while attempting to improve the sugar content of sugar beets, discarded the Galtonian approach in favour of the quantisized Mendel's Law. Nilson-Ehle, when confronted by multiple factors in his investigation of quantitative characters in wheat, used the specific binomial coefficients 1: 2: 1; 1: 4: 6: 4: 1; and 1: 6: 15: 20: 6: 1 to standardize the distribution of his quantisized wheat classes for colour and for size. The most successful analysis of additive multiple-factor inheritance has utilized the step-wise series of binomials indicated by Pascal's triangle in analysing genetic classes. Successive steps give values for additional mutational factors. A paper is in preparation which exemplifies this principle of definite proportions in genetics.

Another paper with graphs is in progress to demonstrate the orderliness of genetic equilibria which are attained toward progressive establishment. Two features may be noted: (1) Successive mutations produce step-wise changes in the proportions of genotypes within a population; these changes are quantisized numerically in time and in direction. (2) There is a remarkable orderliness in the progression of mutant containing genotypes as indicated by the symmetry of the curves charted.

Conclusion

The orderliness of genes; the cyclic position of the atoms within the quantisized subgroups of their polymerized molecules; the reciprocal reversibility of their bilaterally interchangeable phases as oxidation reduction, hydrogel hydrosol, euchromatin heterochromatin; their capacity for autocatalysis and reduplication conditioned by "selectivity" of environmental constituents; the principle of "feed back" giving control to the dynamic equilibria of life phenomena; their ability to "feed forward" by projecting reduplicated and recombined groups of genes to succeeding generations; their mutative flexibility—

these features give life "a most regular and lawful activity, with a durability and permanence that borders on the miraculous" (Schrödinger).

Man holds millions of cards. Does he know how to play them?

REFERENCES

BARTON, W. K. (1951). The theory of crystal growth. Penguin Books.

BEADLE, G. W. (1945). Genetics and metabolism in Neurospora. Physiol. Rev. **25**: 643–63.

JONES, H. S. (1951). The origin of the solar system. Endeavour **10**, 39: 119–25.

NAGEL, ERNEST (1952). Automatic control. Scientific American, Sept.: 44–7.

SCHRÖDINGER, ERWIN (1951). What is life? Cambridge University Press.

STUMPF, PAUL K. (1953). A.T.P., Adenosine triphosphate. Scientific American, April: 85–93.

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA
VOLUME XLVII : SERIES III : JUNE, 1953
SECTION FIVE

The Implications of Recent Advances in Medical Bacteriology

E. G. D. MURRAY, F.R.S.C.

THE phrase "advances in medical bacteriology" might imply a catalogue of the newer methods claimed to be successful in the diagnosis, treatment, and prevention of infectious diseases. This might have an appeal to a society of practitioners in the various branches of clinical medicine, especially were it in the form of a categorical interpretation of the results in highly technical laboratory investigations. But this simple though laborious utilitarian treatment of the subject, however complete it might be made, would of necessity assume the character of an obsequious commentary.

So it seems to me more suitable to the occasion, and of better purpose, to search for trends indicated by newer knowledge, with recognition of gaps and inherent difficulties, which will allow of inferences and bring forward problems. Furthermore, the failures in applications may thereby cease to be disappointments and become instead a clearer indication of needed investigations. It is important to take this approach, partly not to be wrong but just as much to try to avoid being "right for the wrong reasons."

Everyone will agree that the outstanding feature of medical history in the past decade is the use of sulphonamides and antibiotics. These are products of the bacteriology laboratory and have profoundly changed the significance of many infectious diseases. They have permeated almost every branch of medicine, revising concepts and techniques, and have caught the imagination of the public at large. The extensive and sometimes wild uses they have been put to have revealed their value and their limitations and have introduced unexpected problems.

Sulphonamides have been eclipsed by Antibiotics without being relegated to the "limbo of lost reputations." The term "wonder drugs" was coined for them in the period of their ascendancy, and of itself expresses the hopes they inspired—hopes which culminated in the unfulfilled vanity of some clinicians, who imagined that soon bacteriologists would no longer be necessary. Many chemically defined variants were synthesized to extend their range of activity and lessen

their toxicity. The limits of their effectiveness and the precautions with which they must be used became established and their present application in selected infectious processes was determined. This unsurpassed though restricted effectiveness, the simplicity of their administration, their safety with proper precautions, and their stability, make them the treatment of choice in any but the most fulminant conditions caused by certain micro-organisms. Something is known of their competition for enzymes, making it possible to explain their activity and the development of resistant strains of bacteria, as well as allowing the bacteriologist to inhibit them by the use of para-amino-benzoic acid in specimens to be cultured. However, some observers have noticed their ineffectiveness against very susceptible organisms in cases complicated by the presence of resistant species. To be specific: *Staphylococcus pyogenes* is resistant to most sulphonamides and its presence appears to deprive the patient of benefit of the drug against simultaneous infection with very susceptible *Streptococcus pyogenes*. This has been easily demonstrated in the test-tube by the complete protection of the susceptible *Streptococcus*, from what should be overwhelmingly sufficient sulphonamide, by the presence of resistant *Staphylococcus*. The demonstration opens a field of investigation which might well be illuminating.

At the present time, the treatment of bacterial infections is dominated by the use of antibiotics; so over-reaching is this influence that most patients are treated with one or other of the many antibiotics before ever a diagnosis is made and they are not uncommonly cured. There are claims made of benefit in unbelievable numbers of different diseases and it is very difficult to devise a way of evaluating the situation. No one person can read all the profuse literature to make a critical survey, and I don't know how its volume can be even estimated. An impression of it may be gained by the fact that a drug-house interested in one particular antibiotic has issued a monthly bibliographical list on it for about three years, and in no list are the references numbered in less than hundreds; the largest number I have noticed is 1,348. Even though these lists are not lists of the monthly production of papers, it is impressive that they are quoted to illustrate advertisements in the form of appreciations of the use and activity of a single antibiotic. Fortunes have been expended and re-doubled in the production of these drugs and a perfervid, expensive search is prosecuted to find new ones. Waste-paper baskets are filled with the spate of advertising, samples clutter every physician's mail, sales talk by detail-men is enthusiastic and the competition is frantic. The Nobel Prize has been given in two different years for discoveries of

antibiotics. There is no doubt whatever that the interest and value of antibiotics are stupendous, but who can yet know the truth concerning them?

The attitude of a number of medical practitioners to antibiotics resembles that of Galen towards his Samian Clay. He wrote: "All who drink this remedy recover in a short time, except those whom it doesn't help, who all die and have no relief from any other medicine. Therefore, it is obvious that it fails only in incurable cases." The "wonder drugs" give place to the "Miracle drugs." The chemistry of a number of them is becoming known, and, so far, one is commercially synthesized. Their mode of action is largely unknown, so they are characterized by their source, by the range of pathogenic micro-organisms they kill or inhibit (including bacteria, viruses, rickettsia, and fungi), which is spoken of as their "spectrum," and by their toxicity to man and other animals when administered by various routes. For practical purposes the micro-organisms susceptible to each antibiotic are listed and the related therapeutic dose by the tolerated route is given for those of suitable character. But the most noteworthy tendency in recent literature is the emphasis on untoward effects exhibited by all of them, though penicillin might reasonably be excepted. The disadvantage in some is intrinsic toxicity while others interfere by eliminating the normal regional bacteria, which may be classed as friendly, and some encourage local or generalized fungus infections, *Candida albicans* for the most part. There are indications that certain of these effects are linked together and in certain instances may involve vitamins. The warning note is a healthy sign of the approaching assignment of antibiotics to their proper place in the treatment of disease, with a reasoned caution replacing an exuberant enthusiasm.

What particular diseases any antibiotic will or will not cure is a matter of trial, and this information is purely adventitious. But what physiological processes make pathogenic spirochaetes other than *Leptospira* susceptible to penicillin and what these have in common with a number of unrelated kinds of other susceptible bacteria are questions yet unanswered, because the answers involve knowledge of vital processes not yet appreciated. That susceptibility or resistance to penicillin depends in part on the possession or not of penicillinase is insufficient explanation, because comparable contrasts and similarities are found for any other antibiotic, for which no destructive enzyme has been found. There are, too, overlappings and divergencies in the ranges of action of different antibiotics, as well as synergisms and antagonisms between them, and it is not simply a matter of

what one drug won't do another will, but rather of an interference in vital processes, perhaps at different stages or perhaps of different functions. There are intriguing possibilities of identified bacterial breakdown products of some antibiotics (chloromycetin) substituting for amino-acids in the synthesis of proteins and of antibiotics competing with natural substrates in bacterial enzymatic systems. The unexplained stimulation of bacterial and even animal growth by sub-bacteriostatic doses of antibiotics (e.g., terramycin and aureomycin) and discrepancies between *in vitro* and *in vivo* effects on pathogenic bacteria, indicate the need for consideration of the drug-to-host as well as the drug-to-parasite relationship. This aspect of the question seems to me the most important as well as the most interesting raised by the study of antibiotics, and solution of it will probably prove most stimulating to new ideas.

Bacteria are living cells possessing all the latent capacity of evolution, which did not cease immediately Darwin described it. The widespread use of different antibiotics is bringing about profound changes in the environment of parasitic bacteria, whether they are pathogenic or not. This is indicated, for example, by the finding of known bacteria in unusual places and by the disappearance of expected kinds from accustomed places. What disadvantages may accrue from the disturbance of synergistic and symbiotic associations are merely hinted at present; among others, deficiencies of Vitamin B and Vitamin K, or the preponderance of *Proteus* in the gut with the suppression of enterococci, are associated with use of an antibiotic. But the influence attracting most attention for the moment is the increase of resistant strains of pathogenic species previously susceptible to a particular antibiotic and there is even development of dependent strains. Whether this influence is of genetic significance or is the re-development of an atavistic potentiality intrigues some of us, while others are merely bewildered by the practical implications.

These various considerations stir the imagination. The stupendous life-saving achievement of antibiotics and the new aspect, compared with their historical character, imposed on several ravaging diseases, such as lobar pneumonia, all forms of meningitis, syphilis and others, is enormously encouraging. But there is a sobering effect in the momentous possibility that the situation might conceivably be reversed again. Parasitic and pathogenic micro-organisms evolved in the course of time, with natural selection, achieving remarkable host specificities and great pathogenicity, but occasionally some degree of mutual tolerance or even mutual aid has developed between host and parasite. Even in recorded history, syphilis and tuberculosis have,

like other diseases, been seen to undergo astonishing modification in severity and it must be supposed that organisms normal to our bodies now may not always have been so. The struggle for existence imposed by the environmental changes we are inducing rather carelessly and the evident capacity of bacteria to take advantage of their quick succession of generations, may well result in new races of unsuspected characters, and may revive the severity of old known diseases or bring about new ones.

You would call it an unwarranted flight of the imagination were I to predict a return of syphilis to its fifteenth-century fulminance—unlikely because *Treponema* has not been shown to develop antibiotic resistance. Yet there is more than enough to be disturbingly indicative in the prevalence and severity of staphylococcus infections during the past four or five years. Whether there are new diseases developing under our eyes is a question which could be argued without decision. There is much interest in epidemic diarrhoeas caused without doubt by an *Escherichia coli*, indistinguishable from everyone's everyday "B. coli" except by its immunological antigenic configuration. I well remember when nearly all Europeans visiting Egypt suffered from "Gyppy Tummy," although some of the most competent bacteriologists of the time could only find ordinary "Bacillus coli" and no known pathogen. They searched well and were as good as any of their kind today, but antigenic analysis was not developed then to its present state. Is the present troublesome diarrhoea a new disease or an old one better differentiated? The same difficulty is met with in other instances.

There is clearly a growing interest in the structure of the bacterial cell and with it a concern with intra-cellular physiology. For the present I may omit consideration of this subject as beyond the confines of medical interests, but the study of the effects and processes of bacteriophage virus infections of bacteria will one day intrude into the medical field, on the basis of established principles. Not unrelated is the question of bacterial genetics and, though there may still be some uncertainty about actual crossing between bacterial cells in the form of conjugation, there is exciting evidence of what may be loosely called genetic exchange or transference. It has been shown beyond question that single, strictly identifiable, somatic antigenic characters have been transferred hereditarily from one species to another closely related species, in which they did not exist before. The other natural antigenic characters of the recipient species remain undisturbed and, so far, such identifiable marks of distinction can only be transferred one at a time, under closely limited conditions.

It has been claimed elsewhere that crossing explains changed physiological characters and that heritable mutations can be induced by various means. All this is matter of great importance as it involves the previously maintained fixity of immunological types within the species, upon which rests complete identification of bacteria and many epidemiological investigations and concepts. It foreshadows possibilities I hesitate to implicate, but which urgently crave examination in order that we may know whether the process is limited to Types within a species, or may concern nearly related species, or embraces wider taxonomic groups. It is devoutly to be hoped that some crosses, if such they be, turn out mules, lest there prove to be too much too new and too suddenly.

Meanwhile we know enough to identify most bacteria, and many rickettsia and viruses, and to recognize the diseases they cause. General interest in the now well-known presence of sylvatic plague in the prairie rodents has been lulled to oblivion and only wakens briefly with the sudden appearance of a rat in Alberta. Of more recent concern is the invasion of rabies in the wild life and dogs of the Northwest Territories, whence it has spread into the neighbouring provinces. This preoccupation is perhaps because the cry "mad dog" strikes the same frightening note as "Leper" did in the Middle Ages, but with more justification. Along this line of inquiry, there is perhaps more importance and even urgency in the discovery of tularaemia in the beaver and muskrats, with recognition of its spread through the western provinces and into Ontario, as well as through the border states. The spread of this infection in these animals has been recognized only fairly recently, and together with the discovery that *Pasteurella tularense* can persistently contaminate water, it is sufficient to be alarming. The great variety of susceptible hosts, the different arthropod vectors, and the assorted sources of human infections add weight to the warning. The proven arthropod blood-sucking vectors of this disease have a Canada-wide distribution and what others of our large and small wild mammals and birds may be already infected has yet to be discovered.

Closer co-ordination of human and veterinary medicine is evidently most desirable. In addition there is need for extension of the much-neglected study of diseases of our wild life, which should not be confined to fur-bearing animals and game.

I hesitate to embark on the relation of ACTH and cortisone to infection and immunity. There is strong evidence of suppression of antibody production as well as instances of the intensified generalization of infection by their administration. Some maintain that ful-

minant purpuric meningococcus septicaemia is an expression of damage to the suprarenal cortex but I do not find the evidence so far adduced convincing. Experimental animals are certainly rendered more susceptible to meningococcus infection by cortisone. In the human cases no upset of the potassium and sodium balance has been found yet, and many cases show no damage to the suprarenals at autopsy, though some do; also, the blood pressure is often raised to start with though collapse supervenes later. It might just as well be an initial hyper-active suprarenal cortex with subsequent suppression that is responsible for these fulminant cases and for the fact that some are benefited by cortisone late. I decline at present to become involved in the theory of "Stress" and I almost dare not use the word in any of its several dictionary senses, since in some quarters it is becoming almost synonymous with *disease*, even including infections.

The propagation of viruses in tissue culture represents a realization of the present and a promise of a future which may become equivalent to the pure culture studies of bacteria. The possibilities of rapid isolation and serological typing of at least certain viruses lend hope for more exact epidemiological studies and diagnostic accuracy, which may well lead to great progress in the management of the diseases they produce. The long delay and the uncertainty of recognizing specific immune bodies, developed late in the history of a case, have greatly hampered progress; while diagnosis by infection of susceptible experimental animals has been beyond the means of any but special research undertakings. This is one of several interesting applications of tissue cultures and, although most of them do not yet come within the scope of this review, the possibilities extend beyond the field of animal viruses.

In submitting this review I have not attempted an exhaustive analysis of advances in bacteriology of medical significance and I have purposely left out all questions of immunology. I am fully aware of many shortcomings which those with medical knowledge will readily recognize. I have used my experiences and general information without documenting every statement with citations from the literature, in order to avoid a stilted presentation.

The purpose of the instances selected and the interpretations put upon them is to show that there are principles of wide biological significance to be gleaned from microbiological studies. Much has yet to be learned before we can "expound the forms of savage creatures and their deadly injuries which smite one unforseen and the countering remedy for the harm."

TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA

VOLUME XLVII : SERIES III : JUNE, 1953

SECTION FIVE

The Use of Plant Material in the Recognition of Northern Organic Terrain Characteristics

NORMAN W. RADFORTH

Presented by G. KROTKOV, F.R.S.C.

IN recent years emphasis has been placed on the importance of muskeg as a major land type in Canada. Aware of this, the writer and his associates have been concerned with a fundamental method of reference for muskeg. Adequate description of the medium proved difficult because definition must not only relate to material, but also to conditions or states to which the material and the environment contribute separately and in combination. The significance of this complexity has been indicated elsewhere when, for engineers, consideration was given to the principles on which a system for muskeg classification should be built (Radforth, 1952). There, the author proposed and utilized vegetal coverage classes and combinations of these to assist in demonstrating variation in the living component of the organic terrain.

Here, emphasis will be placed on the recognition of botanical relationships in connection with the defining of cover type and subsurface features within the organic terrain. If such relationships among plant components, living and fossilized, are manifest, two major needs will be satisfied. Relationship between characteristics of subsurface and surface organic terrain will be easier to predict and assess, with assurance that generalizations in the field will be more reliable. Also, it will be possible to assess, evaluate, and map conditions associated with terrain change over large areas, particularly for purposes of airphoto interpretation.

Form Differentiation in Vegetal Coverage

The northern organic terrain providing the greatest number of problems for the field worker falls within the taiga of the Churchill area of Hudson Bay. Between The Pas and the Churchill area in Manitoba for a distance of over five hundred miles, organic terrain is by far the predominating type. South from Churchill on Hudson

Bay, it extends for distances exceeding twenty miles with no interruption and even where finally broken regains characteristic continuity beyond the intrusion.

In these regions, an observer has little difficulty in recognizing a marked peculiarity in vegetal coverage, even though he lacks experience with northern muskeg. There are frequently abrupt character changes in the vegetation. This has the effect of marking out or delimiting discreet areas of vegetation with contrasting character. The observer finds it convenient to make use of these areas as descriptive references. However, when asked to explain the qualities by which detection of difference has been claimed, his reference terms are likely to be ill defined, often intangible, and inconsistent. This is particularly the case when the observer is not trained botanically.

Preliminary analysis of the basis leading to detection suggests vegetal form, not species distribution, to be the important agent. Sometimes, topographic and other physiographic factors are influential but usually in a secondary sense.

Following extensive ground and air survey over wide areas of northern muskeg, the writer has found it convenient to establish a classification system referring to relatively pure categories of vegetation (Radforth, 1952). Nine fundamental classes or coverage types are designated. Each is characterized on the basis of variation of three morphological factors—presence or absence of woodiness, range in stature and, where necessary, texture of the foliose material.

Combinations of these class types furnish the descriptive coverage formula for any given area of muskeg. Class components, each represented by a letter, are arranged in the formula in order of prominence. If present to a degree less than 25 per cent by inspection of the total coverage, the component is arbitrarily not significant.

It will be appreciated that class combinations are more significant as designators of coverage character than are the pure classes, the elementary constituents. For consideration in this account, coverage combinations have been mapped (Fig. 1). The combination formulae apply to areas sufficiently large to allow for comparisons with terrain character and change in terrain conditions. They are proving useful for geographical demarcation in the field, on maps, or for airphoto interpretation. Also, they are suggestive of natural relationship in the synoecological sense.

Of the nine coverage classes necessary to designate construction of the coverage, four (A, B, D, and E) contain essentially woody plants. The remaining classes (C, F, G, H, I) are non-woody. In the former group, all but the first-mentioned class contain plants less than fifteen

feet high. In the latter group no plants exceed a height of five feet and this order of height is rare. Immediately south of the Churchill area, coverage formulae containing Class A (strictly arboreous) or Class B (dwarf tree or tall shrub) may be common (Fig. 2). In parts of the coastal area of Hudson Bay and generally to the north of the arboreous coverage, Classes F, E, H, and I are comparatively prominent (Fig. 1). With the exception of E (shrubs under two feet) all members

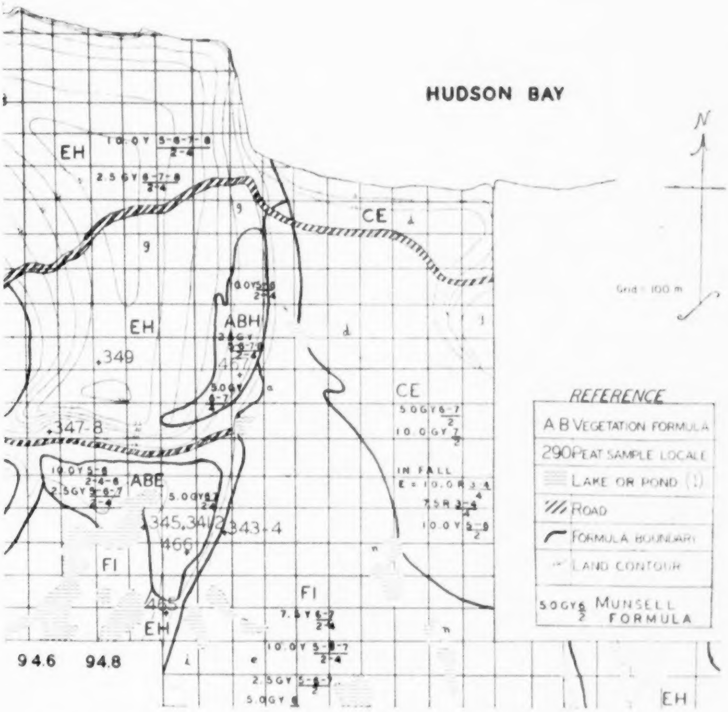


FIGURE 1. Muskeg coverage description map of a coastal area east of Churchill. The spatial relationship between three primary coverage types (E.H., F.I., and C.E.) and two secondary ones (A.B.H., A.B.E.) is expressed.

Topographic symbols (*a*, *d*, *e*, *g*, *i*, *n*) relate to the descriptions established in an earlier work (Radforth, 1952). Among them *d* (rock gravel plain), *g* (exposed boulder), *n* (pond or lake margin sloped) are characteristic of the coverage types with which they occur.

Colour ranges expressed by the Munsell formulae also assist in describing and assessing the coverage character.

of these classes are non-woody: F, eriophoraceous in growth habit; H, lichenaceous, mostly in mats; and I, moss-like, frequently in mats or in hummocks. Beyond the arboreous zone to the south, using the Hudson Bay Railway as a reference axis, treeless barrens are very extensive. Here, combinations of F, E, H, and I cover areas exceeding one hundred square miles, with only negligible interruption by woody plants over five feet in height. The common plants making up these cover zones are listed in Table I.

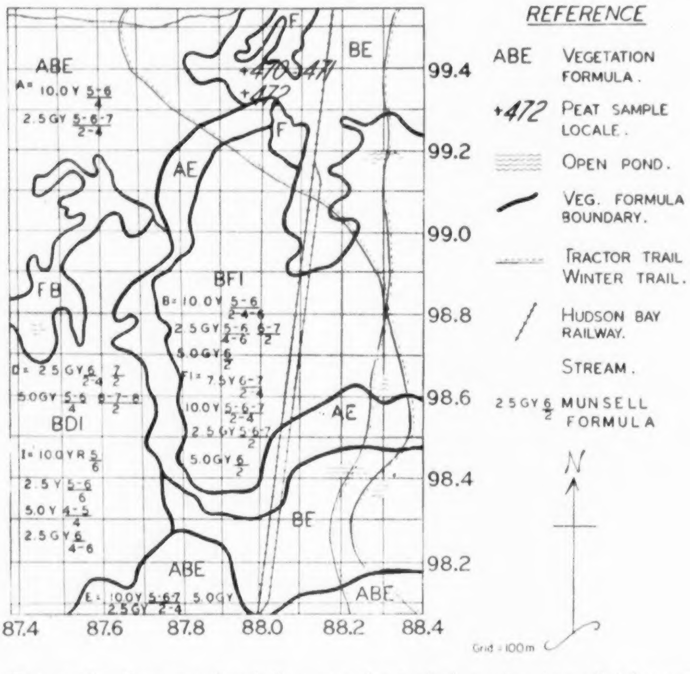


FIGURE 2. Coverage description map for typical muskeg immediately south of Churchill, Manitoba, where dwarf trees and tall shrubs are common (cf. Fig. 1).

The splendid work of Lewis and Dowding (1926) on floristics of more southern confined muskegs, leads one to the conclusion that, for terrain studies, the concept implied in the expression "ecotone" is highly significant. Sometimes borderlines between associations are sharp, sometimes they are ill defined. This also applies to the more northern muskegs. However, ill-defined ecotones are very common,

TABLE I

SPECIES PREDOMINANT IN VEGETAL COVERAGE CLASSES
(Cf. descriptions pages 54–6)

	Class								
	A	B	C	D	E	F	G	H	I
Larix laricina (DuRoi) Koch.	x	xx		x					
Picea glauca (Moench.) Voss.	xx	x		x					
Picea mariana (Mill.) B.S.P.	x	xx		x					
Betula glandulosa Michx.		x		xx	x				
Salix spp.	x	xx		x					
Andromeda polifolia L.					xx				
Arctostaphylos rubra (Fern.) Rhed. and Wils.					xx				
Arctostaphylos uva-ursi (L.) Spreng.					xx				
Dryas integrifolia M. Vahl.					xx				
Empetrum nigrum L.					xx				
Kalmia polifolia Wang.				x	xx				
Ledum decumbens (Ait.) Lodd.					xx				
Ledum groenlandicum Oeder				x	xx				
Rhododendron lapponicum (L.) Wahlenb.					xx				
Rubus arcticus L.					xx				
Rubus chamaemorus L.					xx				
Vaccinium uliginosum L.					xx				
Vaccinium Vitis-Idaea L.					xx				
Calamagrostis canadensis (Michx.) Beauv.			x						
Carex spp.						xx	x		
Eriophorum angustifolium Roth.						xx			
Eriophorum scheuchzeri Hoppe S. lat.						xx			
Juncus albescens (Lge.) Fern.						xx	x		
Epilobium spp.									
E.g. *E. angustifolium* L.							xx		
Pedicularis spp.									
E.g. *P. labradorica* L.							xx		
Petasites palmata (Ait.) Gray							xx		
Petasites sagittata Pursh.							xx		
Senecio spp.							xx		
E.g. *S. palustris* (L.) Hook.									
Hypnaceae spp.									xx
Sphagnaceae spp.									xx
Cladonia spp.									
E.g. *C. coccifera* (L.) Willd.								xx	
C. fimbriata (L.) Fr.								xx	
C. gracilis (L.) Willd.								xx	
C. rangiferina (L.) Web.								xx	

almost characteristic in the north. Often the gradient between associations is so gradual and extensive that it is hard to recognize a mictium. The dynamic nature of coverage development in the north is made increasingly difficult to understand from the floristic aspect because many species are often found which are common to different ecological circumstances. For these reasons the species represented in Table I are difficult to relate by the usual phytosociological methods unless the concept of "life form" is applied.

The evidence presented here seems to indicate that "communities" as interpreted on a morphological basis are clearly delimited. The relationships they seem to reflect (Figs. 1–3) are natural ones, presumably largely controlled by microclimatological, edaphic, and physiographic conditions.

That species can range into different morphological class zones is not unnatural. Seral development may be proceeding at different rates according to the degree of influence of ecological control. The latter may also be responsible for the localized difference in plant stature applicable to many species. A good example of this is ***Ledum groenlandicum*** Ceder which appears to have several stature ranges recognizable ***en masse*** by inspection in the field.

Presence of "form communities" discourages any tendency to regard muskeg coverage as advancing towards a stage when it might be referred to as a "continuum." Subseres, on a form basis, seem to maintain their identity. For those interested in the applied aspects of organic terrain interpretation, this is important. Apparently, discreet zonation of vegetative form may always be expected as a convenience in demonstrating organization and change in the muskeg surface features at all stages of development.

Though it is not within the scope of this account to deal with the use of colour as an interpretive agent in organic terrain studies, secondary reference should be made to its importance. Colour as a variant in terrain coverage character is frequently helpful in identification of class components and delimitation. It is also useful in the comparison of field characters with airphoto records, whether the latter are in colour or not.

The writer finds the best system of colour reference for field use to be the Munsell System (*Munsell Book of Color*) which expresses colour in terms of hue ("relation to red, yellow, green, blue and purple"), value ("lightness") and chroma ("departure from neutral"). Fractions symbolizing values for these components have been used in estimating colour range for different cover assemblages (Figs. 1–3). Seasonal advance must be kept in mind when applying them. However, for a

given time, some shift in colour range is recognizable from one cover designation to another. It is these slight characteristic differences which provide useful collateral in large-scale field survey from the air.

Plant Remains as Aids in Organic Terrain Interpretation

Fossil plants rank high in significance in that they form the major portion of the mass of material in organic terrain. However, their utilization as reference material is limited, unless organized relationship among them is revealed. Technical field investigators and soil taxonomists tend to describe peaty organic deposits as collections of mosses, leaves, twigs, and roots of higher plants which suggest an unorganized heterogeneous mixture of constituents. Published contributions offsetting this attitude are few. Dachnowski-Stokes (1933) has presented the most encouraging account in this regard and his work demonstrates how peaty deposits may differ on the basis of the predominant constituent species. Others have revealed successional organization in peats based on microfossil determinations. However, the former kind of contribution, scarce at the outset, emphasizes constituent species, not constituent plant form units, and the latter utilizes materials which are largely extrinsic. One contributes to peat genesis on a floristic and ecological basis, the other to interglacial and postglacial history of forests and the distribution of tree species.

Neither type of study, though invaluable in its own sphere, lends itself adequately or directly to investigation of the physical attributes and organization on a form range (gross morphological) basis. Form, size, and spatial relationship of macroscopic constituent particles are as important for the applied studies on peats as for an adequate understanding of mineral soils. Also, microfossils to be useful must reveal organization relative to peaty accumulation. To accomplish this, fossil pollen and spore derivatives of intrinsic source must be emphasized in analyses.

Finally, an approach is required which will be appropriate to an adequate definition of muskeg. This the writer found necessary to define elsewhere as "the term designating organic terrain, the physical condition of which is governed by the structure of the peat it contains, and its related mineral sub-layer, considered in relation to topographic features and the surface vegetation with which the peat co-exists" (Radforth, 1952).

The use of macrofossils for interpretation depends upon the purpose to be served. Presence or absence of large members throughout depth in the organic deposit is important to engineers. Bearing potential and other characteristics will vary with this attribute. Whatever the

special need, results depend upon the possibility of classifying the macrofossils as to their size, form, arrangement, and predominance. That variation in size and form does exist will be granted at the outset. How to treat this for classification purposes is not yet fully understood. Variation in arrangement and predominance, if present, may not be revealed on an organized and consistent pattern or series of patterns.

Fortunately, this problem, which is the chief concern of this paper in relation to macrofossils, is not unsurmountable. Its solution lies in the possibility that the record of seral or subseral advance for muskeg is preserved. Since most organic terrain is poorly drained and aerated even in its early history, it is a natural medium for fossilization. Even should seasonal drying, microclimatic change, or edaphic conditions interfere, some record persists. Also, even though certain plants or plant parts disintegrate before or during fossilization leaving no trace of their former presence, field survey indicates that a partial record still remains.

To seek evidence for organized pattern in macrofossil constitution by random selection of gross peat samples is undesirable. Yet this was the method used in all preliminary surveys. The most that the results indicated was confirmation that macroscopically the peats differed widely. Some samples consisted of large interlocking woody conglomerations. Others had a fine-textured matrix that seemed typical for the designation "black muck" used on occasion to define muskeg. The gradient between these two extremes was marked by numerous examples distinguishable on the basis of particle size, form, arrangement, and predominance.

When community development in surface coverage became discernible, search for variation of macrofossil constitution was made accordingly. Significant change in coverage formula was accompanied by evidence of change in macrofossil composition. Though random sampling of organic material was made, it was applied more vigorously wherever surface vegetation pattern changed. Thus, even before discreet surface communities were discerned, indirectly their locations were objectively marked by change in density of subsurface sampling.

As yet quantitative evidence demonstrating macrofossil sample variation with coverage formula is not available. However, descriptive data of a qualitative nature are at hand for several hundred samples. In Fig. 3, coverage formula HE is represented in terms of macrofossil constitution by a predominance of fine-textured, wood-fibrous matrix with associated non-fibrous amorphous matrix. This constitution is interrupted at intervals with discontinuous masses of coarser, mechanically resistant, woody lengths.

For coverage formula AE, the entire mass of peat macroscopically resembles the discontinuous member of HE, except for a foundation of coarse fibrous members varying in size from one-half to one inch in cross-section.

For coverage formula BE, the composition is similar to that for the foundation of AE, with the addition of occasional coarser components as in HE.

Examination of macroscopic content at locations 478 and 479 (Fig. 3), which lie in FI, shows a non-woody fine-textured fibre predominating. This kind of construction is often interrupted by amorphous organic muck and the combined type continues as a background matrix throughout FI, the common coverage for the terrain represented in Fig. 3. Open water occurs only in FI.

Though these descriptions are qualitative in nature they seem to satisfactorily establish the principle that coverage type can be correlated with subsurface macrofossil constitution.

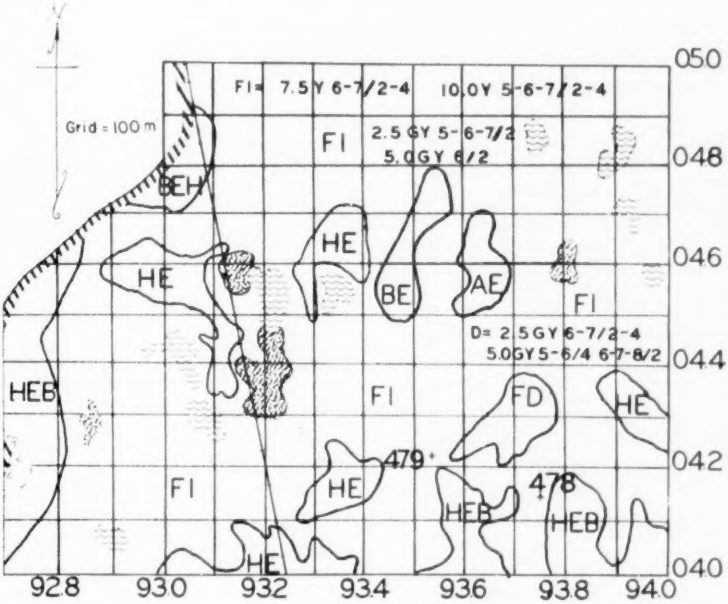


FIGURE 3. Coverage description map for a muskeg type area four miles south of Churchill. The primary coverage is non-woody, less than 2 ft. in height, in discontinuous mats in a mossy matrix.

The level of consistency of the interrelationships expressed is encouraging. This is fortunate, and useful in predicting local terrain conditions. However, there are difficulties, particularly with peat depths exceeding five or six feet. In deep peats, fine-textured, non-fibrous constitution is prevalent in the basal portion which might represent most of the depth of the peat. Also, thickness of fibrous mats and the construction of their components may differ. Spatial relationships between discontinuous secondary units in given types may vary. Similar significant differences occur in given field samples of mineral soils which otherwise compare more or less favourably on a broad basis.

Further evidence of subsurface organization to facilitate prediction of terrain conditions and change rests on the results of microfossil analyses. The writer demonstrated elsewhere (Radforth, 1952) that fossil pollens and spores served as useful indices for reflecting developmental organization in the peat. Seven histogram sets were used. The variants (fossil pollens and spores) were termed index units (Figs. 4, 5). Their frequency was recorded for every two inches of depth as proportions of total counts. Frequencies based on counts higher than 200 did not vary appreciably.

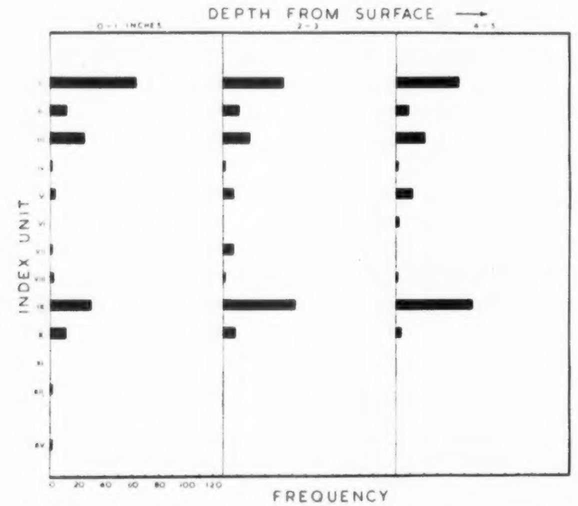


FIGURE 4. Histogram patterns expressing frequency relationships for peats high in Cyperaceous pollens (Index unit IX). The patterns do not change appreciably with depth.

A comparison of histogram results suggests several conclusions:

1. Stable peat constitution throughout depth may occur (Fig. 4).
2. Peats stable in constitution throughout depth may differ in constitution with each other.
3. Some peats, apparently not stable, may reflect a constitutional trend (Fig. 5).
4. Constitutional trends may differ from one example to another.

Intelligent appraisal of these derived observations depends upon a knowledge of the botanical equivalents of the index units, which was not to be found in previous accounts. The botanical designation for each index unit is given in Table II. The somewhat artificial order of listing has been deliberate. It facilitates quick reference in comparing histogram sets.

TABLE II
BOTANICAL DESIGNATION OF INDEX UNITS

Index unit	*Microfossil (pollen or spore)*
I	*Pinus* spp.
II	*Picea glauca*
III	*Picea mariana*
IV	*Alnus*
V	*Betula*
VI	Salicaceae
VII	Ericaceae
VIII	Herbaceous (coverage class G)
IX	Cyperaceae
X	Sphagnaceae
XI	Polytrichaceae
XII	Polypodiaceae
XIII	Equisetaceae
XIV	Lycopodiaceae
XV	Gramineae

Fig. 4, showing a set of histogram patterns which are primarily similar, also shows a high predominance of index unit IX (Cyperaceae) throughout its depth. Where Cyperaceae is relatively high, it is generally the case that there is little evidence for the establishment of a constitutional trend in the peat. When units IV (*Alnus*), V (*Betula*), VI (Salicaceae), VII (Ericaceae), and X (Sphagnaceae) all increase in relation to IX (Cyperaceae) there is also a general similarity of histogram pattern with depth and little suggestion of constitutional change, especially if Sphagnaceae and Ericaceae are unusually high.

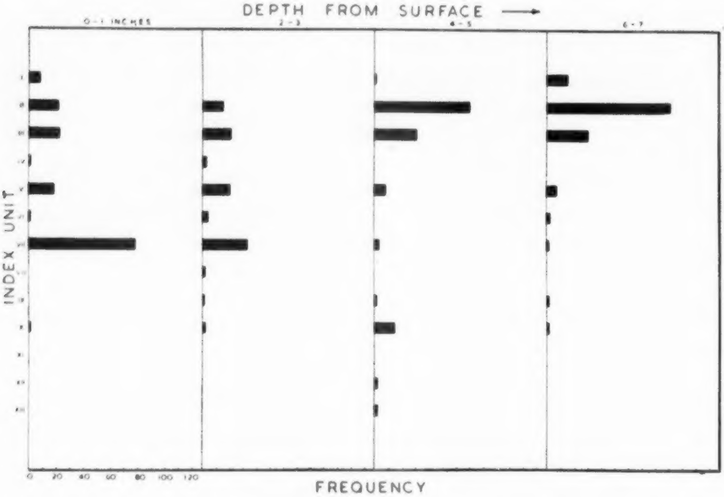


FIGURE 5. Histogram patterns in which relation predominance of index unit VII (Ericaceae) is gradually achieved with decreasing depth of peat. This type of series occurs with E.H. coverage (Fig. 1) and the peat is relatively well drained.

There are of course exceptions. In the case of Cyperaceous dominance, constitutional trends will be evident in the depth scale if topography is irregular even though the amplitude of contour change is only two to three feet. Such changes sometimes occur at intervals of from twenty to a hundred feet.

A similar situation may arise as an exception when Sphagnaceae and Ericaceae are prominent in the sequence of histograms. However, in this case the amplitude of contour change is greater, from two to five feet, often occurring at intervals from ten to fifty feet apart.

Where, in a given set of histograms, there is dissimilarity in the sequence, the constitutional trend revealed in the peat is reflected in the histogram set as a whole (Fig. 5). Here, Ericaceae has gradually moved into relative prominence at the expense of *Picea glauca*.

In Fig. 6, V (*Betula*) then VI (Salicaceae) increase in relative predominance and IX (Cyperaceae) remains steady. Unit VII (Ericaceae) is not prominent at any depth.

The sets of histograms shown in the text figures represent shallow peats. Sometimes top, uncompressed organic matter is several inches to a foot in depth over the more consolidated organic matter below.

Hence the muskeg as it appears in the field ranges from one to three feet in depth. In muskegs varying from three to six feet in depth, microfossil constitutional trends of a secondary nature may be in evidence. However, primary trends in deep peats showing Cyperaceous prominence at any depth maintain this characteristic at all depths (Fig. 4). When Sphagnaceae, Ericaceae, and Betulaceae show relative predominance over Cyperaceae in deep peats at a given depth, this characteristic is generally maintained at any depth. At the moment of writing, the principles outlined here for shallow peats apparently apply for deep peats with the qualification that, for the latter, secondary constitutional trends may become apparent. These represent a measure of botanical instability in muskeg community development. However, their effect is negligible for purposes of assessing organic terrain variation because they do not appreciably change primary microfossil constitutional stability or trend.

Microfossil studies, in signifying the kind of stability or the kind of trend prevalent in the peaty matrix, provide the most accurate and detailed accounts for organic terrain classification and interpretation. Without this detail, it would be unsafe to predict structural change

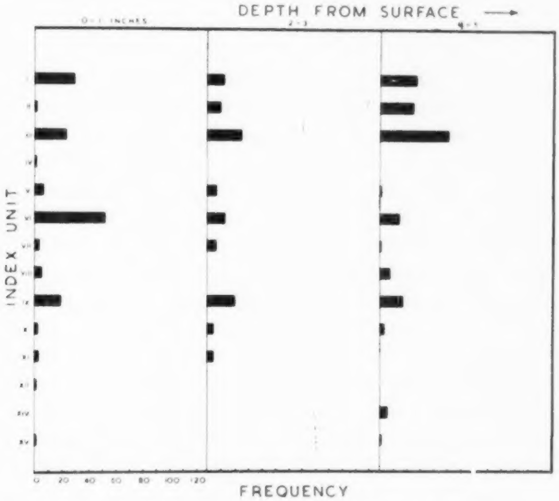


FIGURE 6. Histogram patterns showing change in frequency relationship of microfossil index units with depth. This analysis compares favourably with coverage formulae prominent in dense woody constituents, e.g., B.D.I., Fig. 2.

in the terrain. They are also essential to the establishment of a reliable basis of correlation between surface features and macroscopic subsurface constitution.

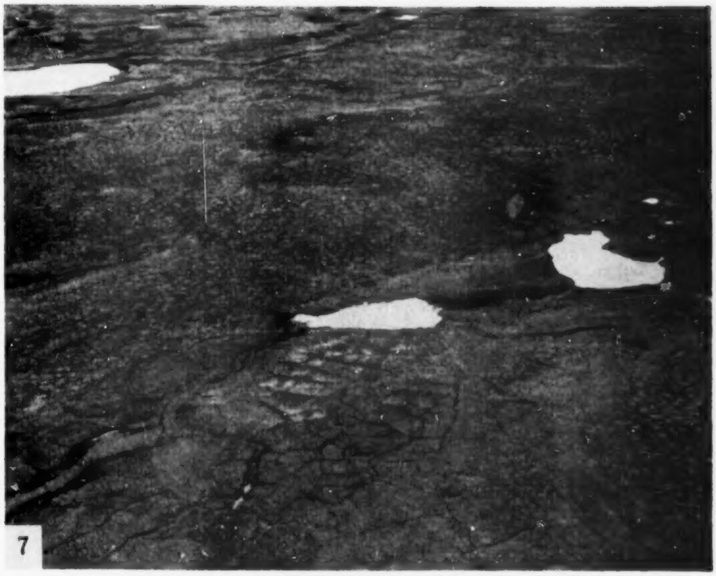
Correlation of Surface and Subsurface Vegetal Data for Special Cases

Though microfossil investigations are fundamental to organic terrain interpretation and to disclosure of organization in peaty material, their contribution is enhanced when considered along with other data. The importance of surface studies and macrofossil survey has already been mentioned. With these it is instructive to correlate any unusual topographic, edaphic, and climatological influence. Also, to assist in aerial interpretation programmes which may follow ground surveys, a knowledge of colour relations in the coverage is essential for best results.

Often a topographic peculiarity in the terrain suggests a problem of muskeg interpretation involving the general appraisal suggested. An example is a type of polygon formation arising frequently in muskeg where permafrost is prevalent. The polygons in Fig. 7 were photographed at an altitude of about 1000 feet when *en route* to Padlei about two hundred miles northwest of Churchill, Manitoba. The detailed study of this type of phenomenon was made about sixty miles to the south of Churchill where the features were typical and the data relatively easy to obtain.

The coverage is also typical for one class of polygon (Figs. 8, 9, 10). Each polygon is ditch-like and along with neighbouring polygons forms a network of depressions, often with abrupt walls except where wind action has uncovered the dead organic remains on the shoulders (Fig. 8). Segments of two depressions are shown in Figs. 8 and 9 with metre quadrat stakes in place. The polygon encloses a peaty plateau with hummocks frequenting the marginal zone (Fig. 10).

The coverage in the depressions contrasts markedly with that on the plateaus. Usually for the former the coverage class is FI and less frequently FD (Figs. 8, 9). For the plateaus the coverage is HE (Fig. 10). The macrofossil constitution throughout depth compares favourably with normal HE coverage (see page 60), except for the upper third (about one foot) of the peat in the depressions where it largely resembles that for FI elsewhere (see page 61). Occasionally where D class becomes influential, the coarse wood-fibrous element invades the peaty matrix.



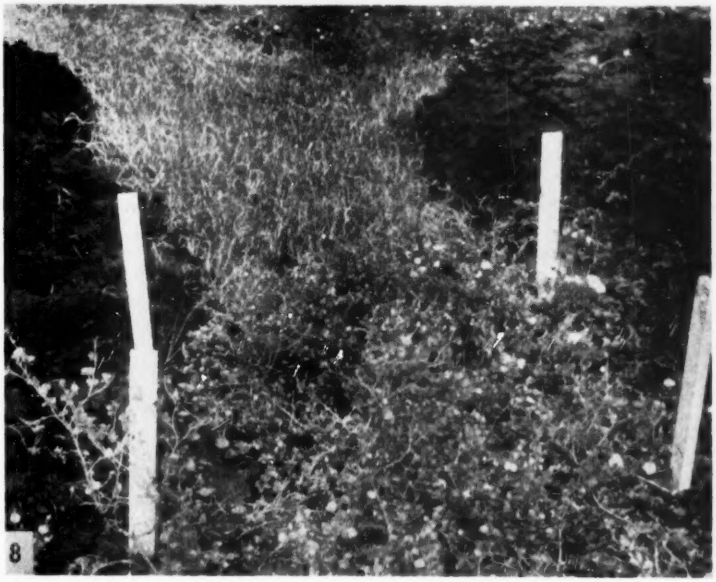


FIGURE 7. Aerial photograph taken at an altitude of about 1,000 feet *en route* to Padlei from Churchill, showing polygon formation in the foreground.

FIGURE 8. A polygon marginal depression showing some F.D. coverage and exposed eroded shoulders of dead organic material.

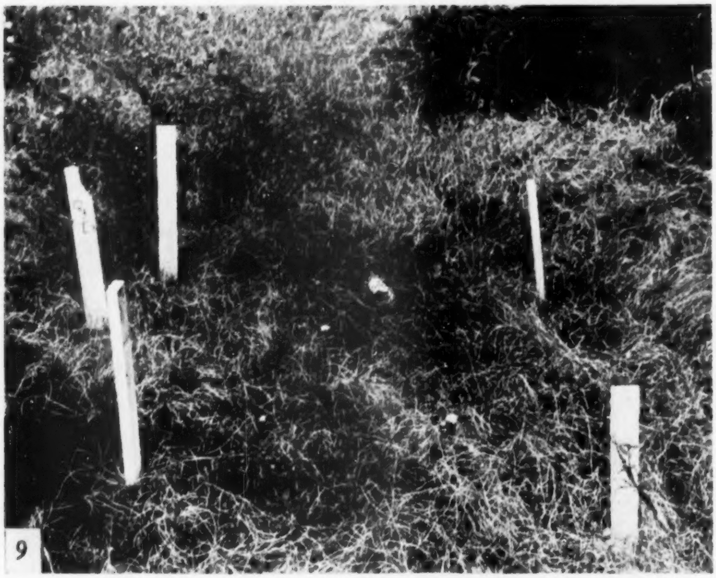


FIGURE 9. A polygon marginal depression showing F.I. coverage. Drainage here is poor as compared with that for F.D. coverage.

FIGURE 10. A type polygon enclosure demonstrating frequent hummocking which occurs with H.E. coverage in the polygon plateaus thirty miles south of Churchill.

Microfossil analysis in the plateaux shows a uniform constitution comparing favourably with that described on page 60 for HE. In the depressions a trend is exhibited in the upper portion in the direction of the constitution described for FI.

The second category of polygons is recognized at once by F and FI class coverage for the plateaux with macrofossil and microfossil constitutions typical for FI coverage. In the depressions the coverage class is DF in the Churchill area, changing to F or I towards Padlei (Fig. 7). For the DF coverage, in the depressions the macro-microfossil constitution exhibits trend; for the F or I class, no trend.

This kind of comparison facilitates conclusions concerning the constructional properties of polygon terrain and its associated physiographical character. The terrain shown in Fig. 10 with HE coverage has with its woody-fibrous constitution relatively good resistance to compressional force and is reasonably well drained. It has a high degree of irregularity topographically, as compared with the type with FI coverage. For the former type the terrain has resilience in contrast with the latter which tends to lose coherence and to dissociate structurally when disturbed.

Comparisons on the basis of coverage alone, though very helpful, are not adequate for predicting polygon terrain conditions. Neither is the combination of coverage and macrofossil constitution. Where class D is promiment in the depressions there is a reasonable mechanical stability to the terrain for the first type of polygon, but not for the second. Drainage is good in the first and poor in the latter. Differentiation between these two on the basis of plant material is only reliable through microfossil analysis. For the relatively stable, better-drained example with DF coverage, the macrofossil constitution will be similar to that for the unstable example. The microfossil histogram pattern would show a relatively high density of Ericaceae-Betulaceae for the approximate lower two thirds of the peat in the case of the former and a relatively high Cyperaceous density for the latter.

Summary and Conclusions

The occurrence of zonation in coverage vegetation provides a valuable aid in interpreting and assessing organic terrain character. In addition, the utilization of zone limits for mapping facilitates an appreciation of terrain change and frequency of change.

It is also significant that the zonation is not based on arbitrary

factors and classification technique. The recognition and use of "form communities" rather than floristic communities does not affect this claim. The grouping of form types as they occur naturally provides a logical lead for subsurface exploration. It also suggests the means by which frequency and distribution of terrain differences may be assessed on an organized basis, from the ground or the air, particularly when vegetation colour range is an accessory interpretive agent.

In only two combinations of coverage classes (HE and FI) does macrofossil constitution seem to be predictable and consistent throughout the depth of the peat. Also, macrofossil constitution for extensive areas is difficult to characterize from small gross samples. This makes terrain interpretation difficult and uncertain unless microfossil constitution is considered.

Microfossils provide the ultimate source of reference and the most reliable source of plant materials in the investigation of northern organic terrain. They are indicators of organization for the vertical and horizontal axes in the organic matter. Through them, detection of constitutional change in peats can be accomplished and assessed. Indirectly they are aids in the study of drainage and other physiographic features.

Finally, and most significantly, microfossils are essential to an understanding of botanical and structural development anywhere in the muskeg. In this capacity, they support the use of vegetal coverage in the classification and prediction studies of terrain interpretation. This is subject to the condition that laboratory analyses of microfossil sequence corresponding to given coverage combinations are consulted fully.

Acknowledgments

The writer is indebted to Miss Jean Evel for her assistance in the preparation of this manuscript and to Edward J. Johnson who as a research technician has provided many of the technical data. Grateful acknowledgment is also extended to many students who have contributed to muskeg studies and to several colleagues, particularly Robert F. Legget, Director, Division of Building Research, National Research Council, to whom all credit must go for initiating inquiry into organic terrain constitution. The National Research Council through the Associate Committee on Soil and Snow Mechanics has provided financial aid along with the Defence Research Board,

through the Arctic Research Section. The latter has shown keen interest in delimitation of muskeg surface character in aerial interpretation studies presently being conducted by the writer.

REFERENCES

AUER, VAINO (1933). Peat bogs of southeastern Canada. Handbuch der Moorkunde, **7**: 141–223.

DACHNOWSKI-STOKES, A. P. (1933). Peat deposits in U.S.A. Handbuch der Moorkunde, **7**: 1–140.

LEWIS, F. J. and DOWDING, E. S. (1926). The vegetation and retrogressive changes of peat areas ("muskegs") in central Alberta. J. Ecol., **14** (2): 317–41.

Munsell Book of Color. Pocket ed., Baltimore: Munsell Color Co. Inc., 1929–42.

RADFORTH, N. W. (1952). Suggested classification of muskeg for the engineer. Engineering J., **35** (11): 1–12.